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Sex and gender effects on power, status, dominance, and leadership – an interdisciplinary look at human and other mammalian societies

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Editorial: Sex and gender effects on power, status, dominance, and leadership – an interdisciplinary look at human and other mammalian societies

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Editorial on the Research Topic
Sex and gender effects on power, status, dominance, and leadership – an interdisciplinary look at human and other mammalian societies

In human societies, men tend to have more power, status, dominance, and occupy leadership positions more often than women; similarly, in animal societies, power and dominance are often unequally distributed between males and females. Despite these similarities across societies of humans and animals, the scientific study of power, status, dominance, and leadership have (for the most part) progressed in isolation, with little cross-disciplinary exchange or fertilization between the natural and social sciences.

In the social sciences, an extensive body of work has investigated the relation between gender (or sometimes sex) and power, status, dominance, and leadership outcomes (e.g., Eagly & Karau, 2002; Goldin, 2014; Eagly and Heilman, 2016; Meeussen et al., 2016; Hentschel et al., 2018; Von Rueden et al., 2018; Smith et al., 2020; Eckel et al., 2021; Shen et al., in press; Heilman et al., 2024). This effort notwithstanding, many questions remain. For example, we lack a comprehensive understanding of the contexts and circumstances that favor (or undermine) women's advancement to powerful positions, and about why and when female and male leaders are evaluated differently (Williams and Tiedens, 2016; Cardador et al., 2022).

In the natural sciences, empirical investigations in mammalian societies have primarily focused on the evolutionary origins and dynamics of male-female power asymmetries. Specifically, such investigations often focus on a few taxa with female dominance, such as bonobos, lemurs, and spotted hyenas (Kappeler, 1993; Lewis, 2018; Davidian et al., 2022;

Smith et al. in this Research Topic). Notably, intersexual dominance–the distribution of power and status between the sexes—is often treated as a binary (i.e., a species is described as either male-dominant or female-dominant) and as a fixed (rather than flexible) trait of a given species (Lewis, 2018; Davidian, 2022). Contrary to this view, recent studies suggest the relative power of the sexes in some animal societies may be less biased in favor of one sex and more flexible than previously assumed (Kappeler et al.).

With this Research Topic, we aim to facilitate academic exchange, to learn from perspectives that typically lie outside of each of our disciplinary boundaries, to draw comparisons and insights across these perspectives, and to promote an integrative understanding of gender and sex[1] inequalities in power, status, dominance, and leadership. To do so, this Research Topic combines contributions from ecology, biology, psychology, and management. It houses a collection of 21 articles, including 10 articles from the social sciences and 11 articles from the natural sciences. We hope this trans-disciplinary Research Topic will not only deepen our understanding of the roots and origins of gender and sex inequalities in humans and non-humans, but also generate new insights into possible solutions for reducing sex and gender disparities.

1 Research investigating gender effects in humans

The papers from the social sciences in this Research Topic tackle three key questions: (1) Why and when are women less likely than men to attain positions of power, status, dominance, or leadership? (2) When and why are women and men evaluated differently in positions of power, status, dominance, or leadership? and (3) Do differences exist in how men and women think, act, and behave in powerful positions? We will provide a short overview of the main findings of the papers in this Research Topic addressing each of these three questions below.

1.1 Why and when are women less likely than men to attain positions of power, status, dominance, or leadership?

The first question about why we see fewer women than men in leadership positions can be answered by considering two perspectives: First, supply-side factors such as explanations for potential gender differences in the pursuit of leadership positions. Second, biases and other barriers women versus men face when deciding to pursue leadership positions. Influences on women's leadership aspirations are explored in the theoretical paper of Gloor et al. Their paper focuses on the early career years as a key period during which positive and negative critical events occur both in- and outside of work domains, such as having a baby or getting a promotion. The authors argue that such events and experiences play key roles in shaping women's leadership aspirations by strengthening or weakening work and non-work identities. They outline the role of contextual factors in shaping the positive relationship between work identity and leadership aspirations. Specifically, the authors argue that a supportive organizational climate and mega-threats in society such as the COVID-19 pandemic can have an influence.

Gender biases in hiring were explored via interviews and a conjoint-experimental study by Dutz et al. Interviewing men and women professors who serve on hiring committees for professorships in STEM (science, technology, engineering, and mathematics), these researchers found that, although applicants of both genders are accorded high status, women applicants often have their ability questioned and receive greater scrutiny. These barriers were revealed in discussions around whether "the job might be too big for them, too difficult, too early" and in openly expressed biased comments such as "can women even do the job?".

Integrating both demand- and supply-side factors via an evolutionary lens, Smith et al. aim to explain why women are less likely to ascend to positions of power and leadership. They review the vast literature across the social sciences and make connections to research on non-human mammalian societies. They propose that men's greater leadership proclivity is rooted in both (1) evolutionary history, such as, sexual selection processes resulting in, for example, men's greater strength and risk-taking, and (2) people's immediate experiences, including institutional climate, gender norms, and socio-ecological factors such as hierarchy steepness.

Finally, Krems et al. investigated if there are different factors influencing when high social status is ascribed to women versus men. As their experimental evidence indicates, a person's gender interacts with their physical features to influence status ascriptions. Specifically, in men physical strength, and in women physical attractiveness, increases attributions of status (which the authors operationalized as expected enactment of anger after being thwarted).

1.2 When and why are women and men evaluated differently in positions of power, status, dominance, or leadership?

Addressing this question about different evaluations of men and women in power, several papers demonstrate the greater negative outcomes that women in high-ranking positions experience compared to their male counterparts. In a study surveying dyads of leaders together with their employees, Van Gerven et al. show that women leaders are more strongly penalized for misdemeanors. Their study indicates that women leaders (more so than men leaders) who display narcissistic behavior, such as arrogance, are perceived as inconsistent and unpredictable by their employees. These perceptions of inconsistency can lead to withdrawal of effort on the part of employees and, along with it, lower job performance.

Feenstra et al. also surveyed women in high-power positions. They investigated outcomes of negative treatment in the workplace, including overt experiences of gender discrimination, denigrating treatment from colleagues and supervisors (e.g., being interrupted,

1 Throughout this editorial, we refer to sex differences in reference to differences between male and female non-human mammals, which are largely biological, and to gender differences when addressing differences between men and women, which is also subjected to social construction.

criticized, or have contributions overlooked), or a lack of mentorship from senior coworkers. Women managers who experienced negative workplace treatment reported the feeling that their position, status, authority, and power were threatened. These internalized power threats were, in turn, related to reduced job satisfaction, emotional exhaustion, and intentions to leave their position.

Importantly, however, powerful women and men are not always evaluated or treated differently. Other papers in this Research Topic identify the contextual factors that contribute to gendered experiences in positions of power. Culture is a key contextual factor. Vink et al. show that in heterosexual couples in which the woman's income is higher than that of the man, the couple's relationship quality suffers. However, relationship quality *only* suffers in traditional gender-stereotypical cultures (e.g., Netherlands, Hungary), but not in egalitarian cultures (e.g., Sweden, Finland). Thus, cultural norms and beliefs about gender in a society can have potent influences on women's experiences and well-being when in a high status position.

A person's age can be a notable demographic variable with the potential to trump gender bias in leadership perceptions. Daldrop et al. investigated the combined effects of a person's age and gender on evaluations of leadership status, prestige and prominence. They conducted two experimental studies in which participants rated people of different ages and genders. Age information indeed outweighed effects of a person's gender. People were allocated lower leadership status when described as young as compared to middle-aged or older.

The specific leadership behaviors also influence evaluations of male and female leaders. In an experimental vignette study, Barthel and Buengeler found that both men and women leaders profited equally from servant leadership (i.e., relationship-oriented behaviors focused on supporting employees), as compared to directive leadership (i.e., task-oriented behaviors focused on communicating clear expectations to employees). Specifically, servant leadership heightened perceptions of leader warmth, morality, and competence but lowered perceptions of leader dominance, ultimately boosting ratings of leader effectiveness and liking.

Finally, Bark et al. show that being representative or prototypical of the team and "being one of us" can help women leaders to overcome gender biases in leader evaluations. Their findings from a combination of experimental and survey methods show that women compared to men leaders benefit to a greater degree from being prototypical leaders. These benefits are apparent in being seen as more authentic leaders and being more trusted by employees.

1.3 Do differences exist in how men and women think, act, and behave in powerful positions?

Vial and Cowgill address the third question of gender differences in how men and women act in positions of power, status, dominance, or leadership. In a stimulating theory paper, the authors argue that women compared to men use power in more prosocial ways intending to benefit others rather than oneself. They argue that this greater prosocial power is driven by women's greater emotional labor: Women more than men tend to regulate emotions to adhere to organizational needs. However, despite resulting benefits for employees and organizations, greater emotional labor has hidden costs for women. It can drain women's energy levels and reduce their likelihood of reaching and retaining powerful positions.

2 Research investigating sex effects in non-human mammals

As our overview above reveals, recent studies in the social sciences tend to focus on the biases and prejudices that women face when seeking or holding power. Instead, the studies of non-human societies that are part of this Research Topic seek to advance an understanding of intersexual dominance relationships–that is, male-female power asymmetries. They do so by: (1) reviewing the available evidence, and identifying (2) its quantitative measures, (3) determinants, and (4) consequences. We will again provide a short overview over the main findings of each paper.

First, Kappeler et al. review the literature on male-female social relationships across the lemurs of Madagascar because, in this radiation of primates, females often dominate males. Female dominance in lemurs was found to be more variable than previously acknowledged and is often, but not consistently, implemented by spontaneous male submission in the absence of female aggression. The ability of lemur females to win agonistic interactions with males develops with sexual maturity, as observed in three different families. This study contributes comparative information on sex roles from an independent primate radiation, thereby strengthening our understanding of the evolutionary emergence of female-biased power.

The study of male-female power dynamics has long faced methodological issues. These limit the ability of researchers to propose objective, quantitative measures of intersexual power that are needed for comparisons across species and for within-species investigations of intersexual power. Addressing this issue, two papers in the current Research Topic sought to identify the best way to measure the social dominance of females relative to males. A paper by Kappeler et al. compared male-female dominance relationships in 9 species of mammals, including 7 primates, rock hyraxes, and spotted hyenas. Their study revealed that the main measures found in the literature, namely the (1) percentage of male-female conflicts won by females and (2) the percentage of males dominated by an average female, are highly correlated across species. Both can thus be used to reliably measure variation in intersexual power. Plotting these measures across species delineates a continuum from strictly male-dominated species to strictly female-dominated species, rather than a simple dichotomy. Their analyses further revealed that in female-dominated societies, submissive signals and gestures are primarily used to establish and maintain dominance, while aggression prevails in male-dominated societies.

In a similar vein, Seex et al assess the accuracy of several measures of intersexual dominance using an agent-based model, in which, unlike in empirical studies, the internal dominance values of individuals are known. From all measures used empirically, the authors conclude that (1) the percentage of males dominated by an average female in a social group and (2) the proportion of intersexual conflicts initiated are the most accurate indices and should be combined.

Several papers in this Research Topic investigated whether the degree of dominance of females over males depends on morphological,

demographic or ecological factors such as relative body size, adult sex ratio, sexual maturity or mating season. The adult sex ratio has been identified as an essential predictor of intersexual dominance both within and between species. One hypothesis that may explain the effects of sex-ratio on intersexual dominance relates to self-organization processes, where a higher frequency of male-male aggression, due to male-biased sex ratios, help females to rise in rank because subordinate males drop to the bottom of the hierarchy (Hemelrijk et al., 2008). This hypothesis is supported by Saccà et al., investigation of wild vervet monkeys, and by Hemelrijk et al. test in groups of rock hyraxes. In vervet monkeys, the intensity of aggression is not higher in males than females but is higher among males when the proportion of males in the group increases. In rock hyraxes, this association is found only in groups with more than one male, where males compete with other males, and females may become dominant over subordinate males.

Proposing an alternative hypothesis for the effect of sex-ratio, Lewis et al. contend that male-female power dynamics are governed by biological market effects due to leverage effects, which occur when members of one sex - here, females - control access to a resource that members of the other sex - here, males - want but cannot take by force, typically ovocytes. Consistent with this hypothesis, they show that in wild Verreaux sifakas, female power increases when their leverage increases, based on the relative value of ovocytes. This effect can happen because they belong to an experienced mother or are scarcer due to a male-biased adult sex ratio.

Several papers on non-human status asymmetries generate additional insights on the dynamics of intersexual dominance. For example, Smit et al. show that even though female mandrills weigh only one-third of the body weight of males, they can outrank some males, especially young males during the mating season, and especially when they are more socially integrated, suggesting some flexibility in intersexual dominance even in the most dimorphic species. Conversely, Koenig et al show in wild gray langurs that male dominance appears inflexible across contexts, and that the rare events of female aggression toward males are aimed at infant protection, while most male aggression towards females occur in a feeding context. This work suggests that intersexual feeding competition may contribute to shaping male-female relationships.

Finally, in the female-dominated society of spotted hyenas, East et al. show that male fitness is substantially affected by the loss of offspring due to infanticide by females. This research counter-balances a classical view of sexual conflict (and of infanticide) in mammals being mostly costly to female fitness, showing that female-biased power can profoundly alter the evolutionary dynamics of sexual conflict.

3 Conclusions

Investigating how gender and sex affect power, status, dominance, and leadership is a truly interdisciplinary science. The collection of articles in this Research Topic represents one of the first steps towards a more unified science integrating the latest knowledge on sex and gender differences in this area across humans and non-humans. Bringing together diverse lines of research can, we believe, catalyze further cross-disciplinary exchanges and foster a broader and more integrative perspective. As one example, social scientists may draw inspiration from the natural scientists' focus on contextual factors that favor the evolutionary or social origins of female leadership, or the biological development of male-female differences. This type of knowledge may offer insights into identifying new pathways towards female empowerment in our own societies. Likewise, natural scientists may leverage the large body of work accumulated by social scientists that highlight the pivotal roles of cultural and institutional norms, and in turn open up new programs of research into animal social learning and norms regarding sex roles in animal societies. We hope this Research Topic can motivate and contribute to innovative and cutting-edge research that span traditional disciplinary boundaries.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Critical events at critical times? A gendered identity approach on the path to (sustainable) leadership

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The early career phase is a key period of identity maintenance and change. But, it is also ripe with important, attention-grabbing occurrences (i.e., critical events) that may modify these processes, particularly influencing women's leadership pursuit. Because previous research has overlooked if or how such events might alter identifying or if these processes differ for people who identify as men and women, we integrate the identity and critical events literatures to elaborate on how positive and negative critical events may shape men and women's identifying in the work- and non-work domains over time. We propose that critical events' effects on identity salience will occur both within and across domains, but that these effects will be stronger within (vs. across) domains. While both positive and negative events can exert negative effects on subsequent identity salience, we propose that the effects of critical events on identity salience may be stronger for women (vs. men). Finally, we connect work identity salience with subsequent leadership status, including contextual moderators that enhance or undermine these effects (i.e., inclusive organizational climate and mega-threats, respectively). We conclude with theoretical and practical implications of this research, including for workforce efficiency and social sustainability. We also highlight calls for future research stemming from our review [e.g., sustainability critical events and gendered analyses for (more) accurate science] as well as fruitful research areas and innovative practices at the work-non-work interface for professionals on the path to leadership.

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gender, shocks, sustainability, identifying, work-family, work-life

1. Introduction

The early career phase comprises critical, time-sensitive periods of career development (Ibarra, 1999; Modestino et al., 2019), and family formation (Grandey et al., 2020; Little and Masterson, 2022). This dynamic period is further shaped by critical events such as receiving a promotion/an award or getting married, which meaningfully affect early career

professionals' identity construction, resilience, and career success (Ibarra, 1999; Blokker et al., 2019; Kraimer et al., 2019). Critical events are important and attention-grabbing occurrences that trigger appraisal, deliberation, and (sometimes) change (Morgeson and DeRue, 2006; Crawford et al., 2019)[1]; they are highly subjective and can originate in the work- or non-work realm[2] with positive or negative valence. While emerging evidence suggests that critical events shape individuals' life experiences, and thus, can also trigger dynamic identity processes that inform people's conceptions of "who they are" (Ladge et al., 2012; Ladge and Greenberg, 2015; Crawford et al., 2019), we lack a comprehensive overview of identity-based processes triggered by critical events during the early career phase.

The critical events literature (Bright et al., 2005, 2009; Seibert et al., 2013; Blokker et al., 2019; Kraimer et al., 2019) is often grounded in stress (i.e., job demands-resources perspective; Bakker and Demerouti, 2007) and motivation theories (i.e., career self-management; Deci and Ryan, 2000). While scholars argue that identity is important to study in its own right (Haslam and Reicher, 2006; van Dick and Haslam, 2012), identity processes also predict concrete career attitudes, choices, behaviors, and outcomes (e.g., job satisfaction, stress and well-being, work effort, promotions, and leadership pursuit; Lobel and Clair, 1992; Bagger et al., 2008; van Dick and Haslam, 2012; Zheng et al., 2021) above and beyond other mechanisms that have received more attention in the literature (e.g., stress, motivation, and/or resources; Deci and Ryan, 2000; Bakker and Demerouti, 2007). In other words, identity-related processes might explain a more modest slice of the explanatory pie in an empirical sense. Yet, we argue that they nevertheless represent an independent explanatory mechanism in a theoretical sense. So, by accounting for these identity-based processes, we aim to provide a more complete understanding of early career employees' paths to leadership.

In doing so, we also explicitly integrate research on gender[3] and critical events. Specifically, we theorize how patterns of identifying differ for people who identify as men and women. Although gender is one of the most significant and sizeable predictors of career outcomes and success (Frear et al., 2019; Zacher et al., 2019; Catalyst, 2020), existing research tends to group men and women together when discussing and analyzing critical events and their effects (e.g., Seibert et al., 2013; Kraimer et al., 2019; Akkermans et al., 2020). According to identity theory, gender is an ever-present, highly visible, and salient identity, modifying and interacting with other identities (Brewer and Lui, 1989; Stangor et al., 1992; Ridgeway and Smith-Lovin, 1999). Yet, much of the research on identity and role transitions–one type of critical event–is qualitative and focuses on only women (e.g., Ladge et al., 2012; Ladge and Greenberg, 2015; Meister et al., 2017) *or* men (e.g., Humberd et al., 2015; Ladge and Greenberg, 2015). Acknowledging the persistent and pervasive gender roles, stereotypes, and social expectations that may modify critical events' effects for men and women—even more so for younger professionals (Eagly, 1987; Eagly and Wood, 2012; Eagly et al., 2020)—we bridge these literatures by including both men and women in our theory building while also proposing if and how critical events' effects on identity salience may differ for early career men and women.

Finally, beyond the individual-level, we also consider two contextual moderators which affect the magnitude of the effect of work identity salience on downstream employment outcomes (e.g., future leadership status): inclusive organizational climate (i.e., organizational cultures that value their members, include them in decision-making, and treat them fairly—regardless of their social group membership; Shore et al., 2011) and mega-threats (i.e., negative, identity-relevant societal events that receive significant media attention; Leigh and Melwani, 2019). We theorize that the former strengthens the positive effect of work identity salience on leadership status while the latter undermines it. With this multi-level approach, we more completely consider employees' everyday realities in context while also opening up new avenues for theory and practice beyond single employees. While individual approaches are indisputably valuable for understanding some phenomena and processes, they can too easily overlook the practices, organizations, and systems within

1 We generally use "critical events" (i.e., distinguishable occurrences) throughout, but we occasionally reference "setbacks" and "shocks" (i.e., "a very distinguishable event that jars employees toward deliberate judgments about their jobs"; Lee and Mitchell, 1994, p. 60), as well as "chance events" (i.e., "unplanned events"; Hirschi, 2010), where relevant. Although their definitions vary slightly, we believe the overarching concept and its potential effects on identifying, career decisions and trajectories are similar enough to justify this cross-fertilization of terms and literatures. See Table 1 for examples.

2 Considering the most common kinds of critical events that early career professionals might experience (see Table 1), the work and non-work (often family) domains seem to be particularly relevant. To be clear, we move beyond the two-domain approach of "work" and "family" to more comprehensively and inclusively reflect other roles from which a person might derive meaning and identity. But, much of the existing, relevant research has focused on "family;" with the rise of dual career couples and the fact that the concurrent periods of family formation and early career which we focus here, much of the work we review and the examples we include still reflects "family."

3 Here, we focus on gender as a binary construct rather than reflecting the more complex, continuous diversity in people's gender identity (see Morgenroth and Ryan, 2018). By using "gender," we mostly relate to cis women and men, largely due to constraints from the literature we review, which used a similarly binary approach. However, here, we proactively acknowledge the continuum of gender self-definitions as well as the multiplicity of gender identities; we also acknowledge the potential limitations that our binary conceptualization of gender might entail (e.g., our theorizing on gender can be affected by who the primary childcare-giver is, if a family is comprised by a couple of lesbian women or homosexual men, etc.).

which these individuals function; in doing so, they also (implicitly) place the onus on individuals to improve their situations (i.e., a "fix the woman" approach; Ely and Meyerson, 2000) despite many factors being entirely out of their control.

In summary, this theoretical framework provides a more holistic understanding of how critical events shape early career men's and women's (future) leadership *via* their dynamic effects on identity salience within and across the work and non-work domains. For a complete overview of our theoretical model, see Figure 1.

2. Theoretical development

2.1. Critical events' effects on identifying within and across life domains

Here, we explain how critical events shape early career professionals' identifying (an ongoing process of identity maintenance and change; Sugiyama et al., 2022), particularly for a specific aspect of identity, namely: identity salience. People possess multiple identities which differ in salience. "Identity salience is conceptualized (and operationalized) as the likelihood that the identity will be invoked in diverse situations" (Hogg et al., 1995, 257). The more salient an identity, the more likely it is to be evoked in a social interaction (Brenner et al., 2014). According to various identity theories (e.g., Stryker and Serpe, 1994; Stryker and Burke, 2000; Epitropaki et al., 2017), people implicitly arrange their identities into salience hierarchies, with more highly salient identities more likely to be deemed situationally relevant and subjectively important (McCall and Simmons, 1978; Ashforth, 2000). Thus, because critical events or "shocks" may be often experienced and trigger important identity processes (see Ibarra and Barbulescu, 2010; Ibarra and Petriglieri, 2010; Crawford et al., 2019) during this dynamic, uncertain early life, and career stage, it is important to understand how critical events shape young women's and men's identity salience.

Despite the more dynamic quality of identity as people grow and develop over the lifespan (Ibarra, 1999; Sveningsson and Alvesson, 2003; Kreiner et al., 2006), people generally maintain a sense of identity continuity to behave effectively (Shamir et al., 1993; Ashforth and Kreiner, 1999; Petriglieri, 2011). That is, initial work identity salience at one point in time should be strongly and positively related to subsequent work identity salience, and non-work identity salience at one point in time should also be strongly and positively related to subsequent non-work identity salience. When critical events occur in the work or non-work domain, it is highly likely that they affect identity salience stronger in the domain in which they occur. For example, if a young woman gives birth or has a miscarriage, the effects of this critical event in the non-work domain may be most noticeable in her non-work identity salience. Similarly, if a young man is fired (or promoted) from his work, the effects of this critical event in the work domain may be most noticeable in his work identity salience. Because shocks research also supports the idea of valence-consistent effects within domains (e.g., Seibert et al., 2013; Blokker et al., 2019; Kraimer et al., 2019), we similarly propose that critical events have stronger effects within its domain of origin.

But, the work–family literature also shows interrelated aspects of work- and non-work-related self-concepts, which may have counterbalancing *or* enhancement effects on identity in the other domain (Wayne et al., 2006; Ladge and Little, 2019). Much research supports the former idea, such that individuals' roles and responsibilities within one domain exert a compensatory effect on

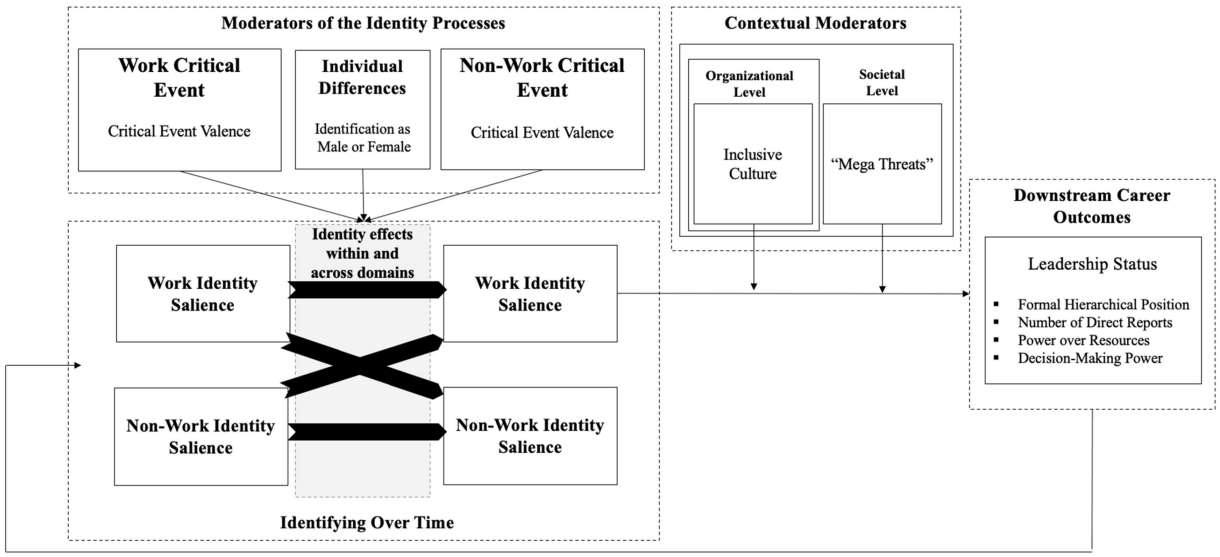

FIGURE 1
Overview of complete conceptual model. The block arrows represent processes.

identity and activities in the other domain (e.g., Bagger et al., 2008; see Greenhaus and Beutell, 1985, for a review), which we refer to as a cross-domain effect. This idea is consistent with the depletion perspective (see Edwards and Rothbard, 2000, for a review; Rothbard, 2001)—a fundamental aspect of work life theories—reflecting the idea that from a fixed pool of resources (e.g., time and energy), engagement in one area reduces the resources available in another area (Lambert, 1990).

While identity is not necessarily a resource, identity salience hierarchies are necessarily structured along subjective importance (McCall and Simmons, 1978; Stryker, 1987; Ashforth, 2000). This implies a trade-off between various sources of identity salience. Indeed, following the "hat" metaphor by Ashforth and Johnson (2001) to describe the relative salience of multiple identities in organizational contexts, one person cannot truly wear "two hats" at the same time. While we do not intend to singularly promote a zero-sum approach to all theorizing on cross-domain effects, at least for identity salience, related empirical research suggests that compensatory effects may be more likely than enrichment effects (e.g., Lobel and Clair, 1992; Bagger et al., 2008). However, admittedly, there is only a paucity of work-family research on cross-domain identity processes in response to critical events.

Thus, we propose that through identifying, a critical event may have manifold effects on identity salience beyond its initial domain of origin to cross-over and impact multiple domains (e.g., work and non-work). We further predict that the effects of an individual's critical event—in the work or non-work domain—resonate more strongly in the domain in which it originated, shaping identity salience more prominently in that domain than potential cross-domain effects.

> *Propositions 1a-b: Critical events affect early career professionals' work and non-work identity salience, particularly* (*a*) *within the domain of its origin* versus (*b*) *across domains.*

2.2. Critical event valence and identity effects

Critical events can be positive or negative in valence. Existing research has shown that critical events tend to have valence-consistent effects within their domain of origin. For example, a promotion is an ostensibly positive critical career event associated with positive career outcomes (Seibert et al., 2013; Blokker et al., 2019; Kraimer et al., 2019). Although these studies were guided by stress or resource frameworks, meaning that positive events triggered their positive effects because they decreased stress or increased resources (respectively), similar claims could also be made based on identity theory for events within domains. To illustrate, a positive critical event in the work domain (e.g., an assignment abroad to gain essential international experience and climb the corporate ladder) may invoke a leaders' work identity, requiring investment in the work role and identity (Crawford et al., 2019; Kraimer et al., 2019), and thus, increases work identity salience. But, cross-domain effects may also occur with an opposite pattern of less magnitude. More specifically, by increasing identity salience in one domain, other aspects of identity become inherently less salient, decreasing in subjective importance (McCall and Simmons, 1978; Ashforth, 2020).

At first glance, negative events may be logically expected to trigger negative effects. For example, if one experiences a major setback at work, they may respond by reducing their work identity salience (and also their work effort, etc.). But in contrast to the valence-consistent effects of positive critical events, negative critical events may also cloud or obscure identity consistency over time, resulting in more variable responses on subsequent identity salience. For example, in a related study of shocks, Blokker et al. (2019) found that positive career shocks strengthened the relation between career skills and outcomes, while negative career shocks undermined this relation. This may be especially likely for early career individuals (Miller et al., 2005) who may reconsider or postpone having children or taking on a mortgage to prevent having "one more worry" during a difficult period (e.g., see Akkermans et al., 2020). Hence, a negative critical event can strengthen identity salience in some cases (e.g., losing one's job may enhance family engagement), but with a broader outlook, they may simply reduce the strength of identity salience within or across domains over time.

This theorizing is also supported by the limited research on critical events and shocks that has considered the role of event valence. Although this work tends to focus on positive *or* negative events (e.g., Seibert et al., 2013) or propose specific effects of critical events regardless of event valence (e.g., Crawford et al., 2019), existing research that has considered both types of critical events shows more consistent empirical support for the valence-consistent effects of positive shocks than negative shocks (e.g., Blokker et al., 2019; Kraimer et al., 2019). Related work on leader identity development also suggests positive events strengthen existing identity salience and identifying processes more so than negative events (e.g., Seemiller and Priest, 2015; Epitropaki et al., 2017).

In summary, we propose that positive events enhance positive, within-domain identity effects as well as the negative, counterbalancing effects across-domains. In contrast, we propose that negative events may generally decrease both effects. The idea that positive and negative events may affect not only the direction but also the magnitude of subsequent effects is supported by theory on critical events (e.g., Morgeson et al., 2015) and empirical research on shocks and chance events (e.g., see Grimland et al., 2012; Seibert et al., 2013; Blokker et al., 2019; Kraimer et al., 2019). Formally:

> *Propositions 2a-c: Critical events' effects on identity salience within and across domains depends on the valence of the events, such that* (*a*) *positive events are more likely to strengthen identity salience in the domain of origin and* (*b*) *reduce it in the cross domain* (e.g., *a positive event in the work domain*

> *strengthens identity salience in the work domain and weakens identity salience in the non-work domain and* vice versa). *Furthermore, (c) positive* (vs. *negative*) *events should generally have stronger effects* (*within and across domains*).

2.3. Critical events, identity salience, and gender

Gender is a fundamental, deeply engrained, and prominent category by which we classify ourselves and others (Hentschel et al., 2019; Martin and Mason, 2022). Gender-based taxonomies emerge already in early childhood with such strength that even the multiple dimensions within one's identity are cognitively nested within gender categories (Brewer and Lui, 1989; Stangor et al., 1992; Ridgeway and Smith-Lovin, 1999). Thus, gender is a highly visible and ever-present identity, modifying other identities which may be more salient.

Following this reasoning, the previously proposed effects of critical events on identity salience may depend on the focal employee's gender. Chiefly important to our theorizing, women may be more sensitive to context than men in their identity formation as well as in their reactions to critical events within those contexts, because they are stereotyped as a minority (e.g., in career roles or at work) and/or they are a numerical minority within the workplace and public sphere domain (Randel, 2002; Gloor et al., 2020). Evidence from identity research supports this idea, as women leaders in male-dominated fields are more strongly impacted by professional and personal identity transitions (Epitropaki et al., 2017; Meister et al., 2017). Because women are more scrutinized while also having to address multiple and paradoxical expectations (Kark et al., 2012; Meeussen et al., 2016; Zheng et al., 2018a,b, 2021), they may be more vulnerable than men, which may translate to stronger effects of critical events on identity salience for women.

A related stream of work-family research shows that men and women have different work-life boundary strength or permeability (Rothbard and Edwards, 2003). According to boundary theory, individuals construct psychological boundaries between different domains in their lives (e.g., work and private life) while also acknowledging that boundaries vary in permeability, namely, the degree to which one domain can influence the other (Ashforth et al., 2000; Kossek et al., 2012; Leslie et al., 2019). These work-family boundaries have been described as more fluid and permeable for women than for men, because of women's relatively stronger need to integrate work and family roles (Rothbard and Edwards, 2003; Halpern and Murphy, 2005; Cheung and Halpern, 2010; Powell and Greenhaus, 2010; Brown, 2015; Braun and Peus, 2018). This suggests that women's work-family boundaries are also likely to be more permeable than men's boundaries. More specifically, women may more strongly identify with both the work and non-work domains, whereas men may relate more to the work domain while also overlooking the need to integrate both domains.

Thus, we theorize that the previously formulated effects of critical events on identity salience both within and across domains may also be stronger for women than for men. Formally:

> *Proposition 3: Critical events' effects on identity salience will be moderated by gender, such that the effects are stronger for early career professionals who identify as women* (vs. *men*).

2.4. Work identity salience and leadership

While identity is an important outcome worthy of study on its own (Haslam and Reicher, 2006; van Dick and Haslam, 2012), aspects of employee identity also predict concrete career attitudes, behaviors, and outcomes (e.g., job satisfaction, stress and well-being, work effort, promotions, and leadership pursuit; Lobel and Clair, 1992; Bagger et al., 2008; van Dick and Haslam, 2012; Zheng et al., 2021). Specifically, the identity literature focuses more on internalized perceptions that build the basis for behavior (see Haslam and Reicher, 2006). So, if a person has a strong work identity salience, they will also behave accordingly to prioritize job-related tasks over others, seek professional development and career opportunities, etc. The leadership literature has highlighted that identity motivates behavior in that professionals who identify as a leader will be motivated to take on leadership responsibilities and search for opportunities to further develop in that direction (Lord and Hall, 2005; Rehbock et al., 2022). Due to this strong link between identity salience and behavioral enactment (Strauss et al., 2012), building theory with an identity lens seems fruitful to enhance our understanding of how changes in work identity salience shape young professionals' work behavior.[4]

To illustrate, if an early career employee experiences a critical negative event in the work domain (e.g., an incident with an abusive boss or an act of harassment), it likely weakens their work identity salience, undermining subsequent leadership outcomes and steps along the way to leadership (e.g., a weakened motivation to lead and/or ambition to apply for more senior projects/roles). Alternatively, if an early career employee experiences a positive critical event in the work domain, such as winning a valuable prize or receiving an early promotion, it likely enhances their work-identity salience,

4 While non-work identity salience could also be theoretically related to subsequent leadership status, within domain effects tend to be stronger and more consistent (e.g., work- or career-identity salience predict work- or career outcomes; Lobel and Clair, 1992). Furthermore, while work identity salience and leadership status undoubtedly have bidirectional effects, and related work on career identity argues that career identity change typically follows employment changes (e.g., Ibarra, 1999), work identity can also precede changes in career trajectories (see Sugiyama et al., 2022).

strengthening subsequent leadership outcomes and steps along the way to leadership (e.g., a greater motivation to lead and/or ambition to apply for more senior projects/roles).

Thus, we focus on how work identity salience predicts subsequent work outcomes related to leadership. While not all employees strive for leadership roles, we have at least implicitly focused our theorizing on early career professionals who have at least some initial leadership ambitions until now, a point that we now aim to make explicit. So, to be clear: while years of time may pass before employees achieve various leadership statuses—and it can also take on various forms (e.g., more direct reports, more power in terms of control over resources and/or decision-making tasks, a position that is formally higher in the hierarchy, etc.; see Figure 1); we keep it intentionally broad here to include related leadership roles, tasks, and leadership responsibilities. Formally:

> *Proposition 4: Early career professionals' stronger work identity salience positively predicts subsequent leadership status.*

2.5. Contextual moderators

Finally, there are also broader elements beyond individuals which may influence if or how professionals' work identity salience affects their subsequent leadership. While non-work identity salience could also be theoretically related to subsequent leadership, within-domain effects tend to be stronger and more consistent (e.g., work- or career-identity salience predict work- or career outcomes; Lobel and Clair, 1992), so we focus again on work-identity salience as in Proposition 4.

We review two key contextual elements here: inclusive culture (i.e., organizational cultures that value their members, include them in decision-making, and treat them fairly—regardless of their social group membership; Shore et al., 2011) and mega-threats (i.e., societal-level critical events, which receive media attention, are negative in valence and identity-relevant; Leigh and Melwani, 2019). Inclusive culture and mega threats are situated at broader levels compared to most of the previously reviewed critical events, which are largely situated at the individual level. Because such higher-level critical events may entail more frequent cues (e.g., more people are involved in or affected by the events, more media coverage of the events, etc.), this makes these contextual moderators qualitatively different from the previously reviewed individual-level critical events, necessitating a new part of our model and conceptual space in our theory-building.

As a first contextual moderator, we integrate recent theorizing on (gendered) identity sensemaking and leadership "imposterism" from Kark et al. (2022) to propose that inclusive organizational climates affect the positive relation between work identity salience and (future) leadership for three reasons. First, in more inclusive organizational climates, demographic factors (e.g., gender, age, motherhood, race, etc.) are not as strongly related to status, facilitating employee evaluations which are more indicative of their ability and potential rather than their visible characteristics (DiTomaso et al., 2007; Nishii, 2013). Thus, inclusive climates may reduce the extent to which those who differ from the societal prototype of leaders (e.g., in terms of gender, age, motherhood, race, etc.) feel that their identity is misaligned with their desired career role (e.g., leadership). Second, inclusive organizational climates are less likely to trigger identity-related sensemaking processes among (future) leaders, because they encourage greater interdependence and mutuality (Ferdman, 2014). Unlike more traditional, highly hierarchical organizations that expect individual, "hero" employees to have all of the answers as they climb the organizational hierarchy (Hollander, 2009); inclusive climates place less pressure on individuals. By definition, inclusion comprises being fully oneself while also allowing others to be fully themselves in the context of engaging in common pursuits. Thus, collaborating is a way that all parties can be fully engaged, and yet at the same time, paradoxically believe that they have not compromised, hidden, or given up parts of themselves in the process. Finally, some organizational initiatives and policies (e.g., if important meetings and events are held in a common language—or perhaps multiple languages, as needed—and within versus after typical work hours, childcare and parental leave offerings, etc.; Gloor et al., 2021a) can also be key signals of organizational inclusion—as well as organizational responses to patterns of organizational exclusion (e.g., higher collective female turnover; Piszczek, 2020).

As a second contextual moderator, we integrate recent theorizing on mega-threats from Leigh and Melwani (2019, 2022) to propose that mega-threats affect the positive relation between work identity salience and (future) leadership for three reasons. Recent years have been peppered with mega-threats at the broader societal level which have undeniable effects on organizations and the people whom they employ. For example, COVID-19 could be a mega-threat for people of Asian descent (because it triggered harassment and aggression toward people of apparent Asian decent), while police killings of people of color could be a mega-threat for people of color (Leigh and Melwani, 2022). Similarly, the recent #MeToo movement (see Gloor et al., 2022b) and the very recent unraveling of women's reproductive rights in the United States (Thomason et al., 2022) might constitute mega threats for women—the latter particularly for women of childbearing age and those who may want (more) children. Of note, mega-threats are negatively valenced by definition, in contrast to the subjectively positive and negative critical events that we focused on previously (e.g., in Proposition 2). Mega-threats like these may play a crucial role in how work identity salience impacts downstream outcomes like a future leadership role, because they increase avoidance behaviors, increase work withdrawal, and decrease social engagement in event observers who share identities with mega-threat victims (germane to the current research, these observers include early career professionals who share identities with mega-threat victims; Leigh and Melwani, 2022). Mega-threats theoretically enact these effects because they

blur work- and non-work identity boundaries (Leigh and Melwani, 2019)—which we previously argued is a reason why women may be more affected by critical events than men (see Proposition #3)—while also trigging vicarious harm and embodied threat (i.e., an appraisal that one is more likely to personally encounter identity-based harm; Leigh and Melwani, 2022). For each of these examples, they are also broader, societal—if not global—events that foster discussions at work, affect multiple individuals with whom one might interact with at work, while also generating widely shared media attention. For these reasons, mega-threats may also have (more) frequent cues.

Thus, more inclusive organizational climate can reduce the negative (and enhance the positive) identifying processes resulting from more individual critical events predicting subsequent leadership status. In contrast, mega-threat(s) can exacerbate the negative (and undermine the positive) identifying processes resulting from more individual critical events predicting subsequent leadership status. But while this theorizing explains how these two contextual moderators shape the dynamic identifying processes proposed in the first stage of our model, we focus our theorizing here more specifically on how these contextual factors affect the (positive) relation between work identity salience and subsequent leadership status. In doing so, we more centrally build on Proposition 4 to further theorize how these two contextual factors may individually affect the baseline positive relation between work identity salience and downstream outcomes like leadership status.[5] Formally:

> *Propositions 5a-b: Contextual factors moderate the positive relation between work identity salience and subsequent leadership status, such that* (*a*) *inclusive organizational climates strengthen this relation, while* (*b*) *mega-threats weaken this relation.*

In summary, we propose that critical events can shape identity salience both within and across domains, but that they trigger stronger effects within (vs. across) domains. While positive events may strengthen positive, within-domain identity effects and the negative, cross-domain effects, negative events may weaken both effects. Furthermore, we propose that these effects are stronger for people identifying as women than for people identifying as men, because women are more sensitive to context and have more permeable work-family boundaries than men, which means that women may react more strongly to critical events than men. We then connect identity salience to important downstream outcomes such that work identity salience positively predicts early career professionals' (future) leadership status. Finally, we also consider contextual moderators that shape the magnitude of the positive relation between work identity salience and leadership status—inclusive organizational climate and mega-threats: while the former enhances this effect, the latter undermines it.

5 While these moderators may also interact with each other (i.e., a more inclusive culture buffers employees from the negative effects of mega-threats; Leigh and Melwani, 2019, preserving the positive relation between work identity salience and leadership status), we focus here on their independent, individual effects as a first step.

3. Discussion

Integrating the critical events and gender/diversity literatures with an identity lens, we explored the idea that positive and negative critical events shape early career professionals' identity salience, particularly within—vs. across—domains, generally triggering stronger effects for women than for men. While we theorized that work identity salience predicts downstream outcomes like leadership, the downstream effects of these dynamic identifying processes in response to critical events are moderated by key aspects of the context: how inclusive the organization is and the presence of mega-threats. Next, we discuss the implications of our model for theory and practice.

3.1. Theoretical implications

First and foremost, we built theory about how critical events affect identifying over time. In doing so, we could more accurately predict and outline the effects of positive and negative critical events and their effects on employees' identity salience. This builds on prior literature that has treated work and non-work (often family) identities as separate (e.g., Greenhaus, 1971, 1973; Amatea et al., 1986; Lobel and Clair, 1992; Bagger et al., 2008). Instead, and in line with more recent theorizing on identity processes at the work-family interface (e.g., Crawford et al., 2019; Ladge and Little, 2019), we theorized that work- and non-work (family) identity salience likely enjoy a process of co-evolution through cross-domain effects, particularly in the wake of positive events.

Second, we also conceptually explored the idea that the effects of critical events are stronger for women than for men. In doing so, we aim to extend existing knowledge of critical events and shocks which has grouped employees together to analyze the effects of critical events (e.g., Seibert et al., 2013; Blokker et al., 2019; Kraimer et al., 2019). By considering gender as a primary identity component and a major aspect of the process through which critical events affect work- and non-work-related outcomes, we may better understand if and how early career men and women respond to critical events. In doing so, this research also aims to complement research in related areas (i.e., critical events and identity transitions), which tends to focus on men *or* women (e.g., Ibarra, 1999; Ladge et al., 2012; Ladge and Greenberg, 2015; Meister et al., 2017; Crawford et al., 2019).

We theorized that women are more susceptible or sensitive to critical events and their identity-related effects than men due to their relatively lower power and status in organizations (Catalyst, 2020; Henningsen et al., 2022) and because of the dual and multiple societal expectations and pressures that women

may experience and internalize in earlier adult ages (Meeussen et al., 2016; as previously described). However, this idea also builds on recent theorizing on the physical, bodily changes that may also make women more vulnerable to critical life events, particularly within this early- to mid-career period (e.g., Grandey et al., 2020). Because women may be more vulnerable at work and more involved in childbearing and rearing at this stage than men (Gersick et al., 2000; Grandey et al., 2020; Little and Masterson, 2022), they are likely more attuned to or affected by critical events, many of which are related to their personal life experiences. Related research supports this idea, because women are also more field dependent than men (i.e., more reactive to external stimuli; Haaken, 1988; Martin, 2000). While this field dependency has been interpreted as a "lack of independent thinking and a regrettable inability to separate one's reactions from contextual influences" (Calás and Smircich, 1992, p. 232–233), this "contextual sensitivity" may also be strength (e.g., see Haaken, 1988). For example, leaders who are more sensitive to context may also perform better along progressively vital social and environmental sustainability outcomes (see Matsa and Miller, 2013; Post, 2015; Byron and Post, 2016). Hence, instead of focusing on women's sensitivity as a weakness to be overcome, it may (also) indicate a need to help men in strengthening their sensitivity to context—including, but not limited to critical events. Indeed, young men may be more influenced by new norms that prescribe men to invest more in their family, suggesting a potential opportunity for change (Meeussen et al., 2016), perhaps especially in the wake of a (positive) critical event.

Considering the greater permeability of work-life boundaries for women than for men, one could also expect gender to function as a moderator for cross-domain effects of a critical event in one domain on identity salience in the other domain. For example, getting married, a critical event in the non-work domain may have stronger effects for women's work identity salience than for men's work identity salience. This is because women may be more sensitive to—and more often confronted with—external expectations about their new role identity as a legal partner and/or a potential parent (see Rivera, 2017; Gloor et al., 2018a, 2021b). Similarly, the latter part of our model might also be more precisely depicted with moderation by employee gender. That is, inclusive climate and mega-threats might be more influential for women (vs. men)—just like the front-end of our model—for some of the same reasons (e.g., women are more sensitive to context and have weaker boundaries between work and non-work domains compared to men) and because women are often the target of mega-threats [e.g., the recent undermining of women's (reproductive) health and rights in the United States]. But, many of these mega-threats are driven primarily by race/ethnicity (e.g., mass shootings, police brutality, and killings of specific groups; Leigh and Melwani, 2019, 2022)—not gender; so, while an intersectional approach may be fruitful here to explain the process and predict leadership outcomes, it becomes quickly complicated due to the multiplying number of categories (e.g., race/ethnicity, plus gender, and oftentimes age) as well as diverging predictions (e.g., for Asian women vs. Black women; see Hall et al., 2019, for a particularly lucid review). Thus, while out of scope here, we encourage future research to more thoroughly explore if and how our model might be depicted (e.g., with an intersectional lens).

Finally, despite increasing research on critical events, shocks, and related concepts, our review of the literature—and thus, also our theory-building—was admittedly limited, because it focused on "typical" professional and personal events (e.g., job loss or childbearing) and largely took a human resource management perspective. Together, these factors limit our understanding of how sustainability affects gendered critical events (and vice versa), as well as the implications of these dynamics for (future) leaders—critical issues to better tackle grand challenges. For example, climate change creates social perils like conflict and extreme weather (Zhang et al., 2007), which may trigger one (or more) critical events; these events may not only differ from those we previously reviewed, but they may also trigger more critical events (see United Nations, 2018; Gloor et al., 2022a). We also know that social and environmental sustainability are deeply related, because vulnerable populations—including, but not limited to women—are more frequently and severely affected by climate change and related issues while women may also be uniquely positioned to lead towards more (social) sustainability (Byron and Post, 2016; Chang et al., 2022; Gloor et al., 2022a; Matsa and Miller, 2013).[6] Given the short timeline to meet environmental goals, paired with widespread global talent shortages (Franzino et al., 2022) and the increasing numbers of (climate) migrants who may be particularly prepared to tackle these challenges, scholars and organizations should not overlook these "sustainability *mega*-critical-events" and their multifaceted implications for theory and practice.

3.2. Practical implications

One recommendation from our research for early career professionals could include active identity-based reflections. In doing so, these early career professionals may grow more aware of their valued identities in various domains, and thus, be better prepared to consciously adapt their self-views, if/when needed (see Roberts, 2005). For example, professionals can implement regular reflection sessions on a monthly or semi-annual basis by answering questions such as "Who am I as a professional?," "What is important to me?," "What (un-)expected events took place and what do they mean to me?," and "How did/do critical events in the past month or year change what I want from my

6 These effects may not only be limited to female leaders of organizations, because prominent examples and research suggest that the critical event of childbearing—when gaining a female child—can also motivate fathers to become more (socially) sustainability (e.g., venture capitalist and billionaire philanthropist John Doerr; Meyer, 2021; see also Cronqvist and Yu, 2017).

career and/or in my personal life?" (see also Rehbock et al., 2021, for suggestions of active identity reflections for organizational leaders). Managers and leaders can support these reflections by introducing them in regular conversations with their employees, annual meetings, etc.

Extending from our theorizing around inclusive organizational climates, leaders (e.g., group leaders, supervisors, and other leaders such as deans and heads of departments in academia) would do well to promote a culture where employees do not feel that they are alone or that they need to decide between their career *or* their personal life to succeed or climb the organizational hierarchy into a leadership role. Because supervisor support strategies often take the form of informal arrangements (Kossek et al., 2016), an open and trustworthy relationship between employees and leaders may help to meet individual employees' needs. However, leaders can further promote inclusion and supportive, compassionate cultures toward employees in their teams (Leigh and Melwani, 2019) by showing value for and acceptance of employees during critical events—and perhaps especially in the wake of mega-threats—for example, by showing commitment to employees' needs (Ladge and Little, 2019) and assuring psychological safety around identity-related discussions (Leigh and Melwani, 2022).

More generally—and building on our brief discussion of workplace initiatives and policies in the previous section about inclusive organizational climate—flexible work arrangements, policies, and practices at the organizational level could also enable employees to balance their multiple needs in work and family domains (Ladge and Little, 2019). To facilitate long-term success, such efforts must be career enabling–rather than career enclosing (Bourdeau et al., 2019)–and offered to *all* employees, ideally in an opt-out rather than opt-in fashion (e.g., see Gloor et al., 2018b; Erkal et al., 2022) to reduce bias and career consequences that may systematically (dis)advantage those from particular social groups. Emerging evidence also suggests that an opt-out approach (vs. the more common opt-in) may also increase qualified women's pursuit of leadership roles (Erkal et al., 2022).

With the broader career scope in mind, and because the largest share of trained female talents is lost (or pushed out) during the early career phase on which we focused, we hope that this research might also inform the persistent and pervasive gender gaps in leadership positions across academia and organizations (e.g., Kossek et al., 2016; Catalyst, 2020; Rehbock et al., 2021; Henningsen et al., 2022). Women often leave and/or are lost after critical events and shocks like the ones we highlighted here (e.g., pregnancy; see Gloor et al., 2018a; Paustian-Underdahl et al., 2019; Zacher et al., 2019; Arena et al., 2022). However, men and women in more advanced career stages or leadership roles can proactively offer support as mentors, sponsors, and allies—by speaking openly about how to successfully integrate multiple identities from the work and non-work domain without having to choose one over the other. Increased awareness of how early career women's and men's identity salience and leadership pursuit differ in response to critical events may be fruitful areas for organizational allyship, thereby facilitating workforce sustainability and advancing more gender balance in representation and power where it is still particularly needed at later career stages.

Finally, some policies show promise to facilitate female retention regardless of the identity processes underway (e.g., reliable and affordable childcare provisions; Piszczek, 2020; or a simple résumé intervention to help women return to work after a caregiving leave; Kristal et al., 2022). Because biased turnover undermines workforce and economic sustainability, innovative approaches may also be fruitful here. For example, one organization successfully retained their employed female talents around a specific critical event—childbearing—by providing all pregnant women with a small, discretionary budget they could use to meet their diverse needs (e.g., hiring a research assistant to monitor data collection while on leave or paying for childcare help)—they only needed to formulate a concrete plan with their supervisor prior to childbirth (Hering, 2019). This approach is flexible to meet the diverse needs of early career female talents, delivered in an opt-out approach while also creating accountability—all of which are effective mechanisms from behavioral science (Bohnet, 2016). Thus, such innovative strategies could also help other organizations to retain early career female talents, fortifying their leadership pipeline, and increasing workforce efficiency more broadly.

3.3. Strengths, limitations, and future research

Two key limitations related to our theorizing are particularly worthy of note. First, conceptually, identity is a vast concept answering the question "who am I?" (Stryker and Serpe, 1982, p. 206). Here, we focused on one specific aspect of identity: salience. Thus, we encourage future research to expand beyond this singular, albeit critically important and influential, facet of identity. While identity centrality is a more stable aspect of identity which may be less affected by the context—including, but not limited to—critical events (Kreiner et al., 2015), posing challenges for theoretical and empirical work, the concept of misidentification (i.e., internal identity asymmetry; see Meister et al., 2014, 2017) might provide fruitful grounds for both types of research.

Second, critical event valence is a key factor related to the form and magnitude of effects on identity salience. While valence can be very subjective, we largely focused here on the more normative interpretations of key critical events (e.g., in Propositions 2a–c and Table 1). While we believe this event-oriented approach (a la Morgeson et al., 2015) represents a conceptual and methodological improvement by disentangling cause and effect compared to existing shocks research which tends to conflate event valence with its effects (e.g., an event is considered to be "negative" if it has a negative effect on a downstream career outcome; Seibert et al., 2013; Kraimer et al., 2019), this approach also represents an oversimplification of reality. To remedy this, we encourage future research to prospectively analyze critical event content and individuals'

TABLE 1 Overview of examples of key (Early Career) critical events.

Critical events	Valence	
	Positive	Negative
Work Domain	(Early) Promotion	Passed Over for Promotion
	New Position/ Employment	Contract Ending
	Further Education	Job Loss
	Award/Honor for Achievements	Act of Harassment/ Discrimination
	Career Choice (Desired)	Career Change (undesired)
Work- and Non-Work Domain	(Available) Parental Leave	(Lack of/Too Much) Parental Leave
	Moving (Desired)	Moving (Undesired)
Non-Work Domain	New Relationship	Separation/Divorce
	Moving in with a Partner	Forced Removal from One's Home
	Sabbatical/Decision to Travel	Health Issues, Accident
	Marriage	Death of a Loved One or Partner
	Pregnancy/Having a Baby	Having an Abortion/ Miscarriage

The aim of this table is to provide a clear overview of some key examples of early career critical evens originating in various domains that may be normatively positive or negative in valence. However, that these events are highly subjective and not always uniformly experienced as positive or negative; we tried to explicitly account for this in some cases (e.g., parental leave can be quite positive for women's health and recovery after having a child, as well as men's and women's bonding and adjusting within the family; but, it can also be quite negative for one's workplace experience and trigger negative career penalties—particularly with longer maternity leaves; e.g., Gloor et al., 2018a; Hideg et al., 2018). However, we also explicitly acknowledge the trade-off between trying to build inclusive theory—generalizing to a broader number of events in our theorizing—while also attempting to accurately depict (the average) individual's experience(s).

subjective evaluations of event valence separately from their subsequent effects on various outcomes (e.g., identity salience, leadership status, etc.).

Beyond individual identity processes, structural shocks may also influence more relational and collective identity processes. For example, there are three different levels of self (Brewer and Gardner, 1996; Brickson, 2000), which are triggered by the context in ways that can affect identity salience. The personal self refers to the individual level of the self-concept, mainly focused on one's characteristics, attributes, and self-interest; the relational self is derived from dyadic and small group relationships, as well as from the roles individuals hold in relations to others (e.g., manager, employee, etc.). Thus, this aspect of identity is mainly focused on the responsibilities and responsiveness that comes with their roles and relationships towards others' needs. This more collective self is based on the individuals' connections to a collective, a group or wider community (e.g., organization, state, country, etc.) and is mainly focused the obligation and commitment to the group's welfare (Brewer and Gardner, 1996). Following this logic, different critical events and the associated identifying processes do indeed affect individual employees across these multiple levels. Thus, changes in the social structure, manifested in changes in relationships (e.g., organizational layoffs or restructuring of many colleagues), can also influence early career professionals' identity salience. These changes can influence the relational levels, but also the collective level (e.g., if a person leaves the organization or takes a leave of absence due to some critical life event), possibly reducing early career employees' work identity salience. Future research is needed to more thoroughly explore and test these ideas.

Similarly, men and women often have partners who also work (i.e., dual-career couples; see Crawford et al., 2019). Thus, while we focused on individual men and women in our theorizing, it is also possible that the critical events and the subsequent identity-related processes triggered by these events also affect the focal men or women's partners' identity salience. While new research by Little and Masterson (2022) considered the direct, indirect, and shared crossover mechanisms of specific critical events (e.g., having a child and returning to work) on organizationally-relevant outcomes grounded in resource- and stress-based theories, sensemaking processes at the partner-level may also facilitate identity-spillover effects among couples (see Crawford et al., 2019). Thus, even if critical events more strongly affect women's identity salience, they may still meaningfully affect women's partners (often men) and these partners' identity salience, as well.

Finally, previous research has called for explorations of gendered effects in the context of critical events or shocks (e.g., Kraimer et al., 2019); here, we take this request one step further: at a minimum, future research should not only consider the potential main effects of gender or including it as a covariate, but scholars should also consider its potential moderating effects. In light of our Proposition 3, for example, it could be that the previously reported effects of critical events or shocks not only differ for men and women but may be entirely driven by women. If true, this is no minor issue, because social scientists' inaccurate over-generalizations about empirical findings—even if unintentional—impedes progress in our understanding of empirical phenomena *and* social justice gains in terms of assessing and improving professional experiences and career progression for more equity in leadership positions and in organizations more broadly (see Eagly, 2016).

4. Conclusion

We theoretically explored the effects of critical events on early career professionals' work- and non-work identity salience over time, including if these effects differ by event valence or for men and women. We further considered the effect of work salience on (future) leadership status, including the roles of inclusive cultures and mega-threats. Thus, this theoretical work highlights key insights for a more holistic understanding of early career

professionals' work- and non-work experiences and their identity-related effects, such that not all critical events may trigger changes over time. Instead, positive (vs. negative) critical events may trigger stronger effects on women's (vs. men's) identity salience within (vs. across) domains—especially in less inclusive climates and/or in the presence of mega-threats—with implications for leadership pursuit and (social) sustainability more broadly.

Author contributions

JG, SR, and RK contributed to the conceptualization, writing—original draft, and review and editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

SR is now employed by Talent and Organization, Accenture Strategy and Consulting.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Sure you are ready? Gendered arguments in recruitment for high-status positions in male-dominated fields

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Recruitment contexts such as STEM professorships promote clearly defined selection criteria and objective assessment. We illuminate in these contexts, the subjective interpretation of seemingly objective criteria and gendered arguments in discussions of applicants. Additionally, we explore gender bias despite comparable applicant profiles investigating how specific success factors lead to selection recommendations for male and female applicants. Implementing a mixed methods approach, we aim to highlight the influence of heuristics, stereotyping, and signaling in applicant assessments. We interviewed 45 STEM professors. They answered qualitative open-ended interview questions, and evaluated hypothetical applicant profiles, qualitatively and quantitatively. The applicant profiles enabled a conjoint experiment with different applicant attributes varied across the profiles (i.e., publications, willingness to cooperate, network recommendation, and applicant gender), the interviewees indicating scores of selection recommendation while thinking aloud. Our findings reveal gendered arguments, i.e., questioning women potentially fueled by a perception of women's exceptional status and perceived self-questioning of women. Furthermore, they point to gender-independent and gender-dependent success patterns, thereby to potential success factors particularly for female applicants. We contextualize and interpret our quantitative findings in light of professors' qualitative statements.

KEYWORDS

STEM professorships, recruitment, gender, heuristics, stereotyping, signaling

Introduction

Men continue to occupy most high-status and influential positions in the world of work (see, e.g., Catalyst, 2020a,b; Levanon and Grusky, 2016). A driver of sustained gender inequality are gender biases in recruitment evaluations based on stereotyped beliefs (Heilman, 2012; Koch et al., 2015; Begeny et al., 2020). Clearly defined selection criteria that are objectively assessable have been suggested to counter such gender biases (Heilman,

2012). For example, in academic recruitment for professorships, the strict regulations of public authority and clear output/performance indicators can be seen as largely objective leaving no room for gender-biased interpretation. Yet, particularly in the STEM fields (science, technology, engineering, mathematics) men continue to occupy the majority of professorships (e.g., GWK, 2020; McCullough, 2020). We argue that, even in contexts promoting clearly defined criteria and objective assessment, such as academia, these criteria can be subjectively interpreted and construed differently for men vs. women, leading to gender-biased evaluations (van den Brink and Benschop, 2012; Herschberg et al., 2015). To illuminate gender (in)equality arising from subjective interpretation of seemingly objective criteria, we investigate how gendered arguments find their way into the assessment of applicants for STEM professorships.

In recruitment for STEM professorships, as in recruitment for other high-status jobs in male-dominated fields, stereotypical perceptions of who fits a position favor men (Heilman, 2012; Carli et al., 2016; Dutz et al., 2022). Due to gender stereotypes, women are considered a "risky" option (Fleming Cabrera, 2010). Research on professorial recruitment shows that female applicants are evaluated based on a "proven masculine success model" (van den Brink and Benschop, 2014, p. 17), thus, on different standards than men. Additionally, research shows that academic "excellence," as halo selection criterion, is a gendered construct and subjectively discussed (van den Brink and Benschop, 2012). Research on heuristics and stereotyping enlightens how various biases influence recruitment; based on stereotyped heuristics, women and men are generally ascribed different qualities, and their behavior is interpreted differently (e.g., Rudman and Phelan, 2008; Heilman, 2012). Stereotype biases further reduce perceived fit, particularly when the stereotypical image of traditional job holders (male professors) does not match the applicant's gender (Tversky and Kahneman, 1974; Heilman, 1983, 2012). This phenomenon extends to self-assessments as stereotypes influence which qualities women and men under- or overestimate in themselves (Heilman, 2001; Hentschel et al., 2019). Therefore, evaluators may assume that women feel uncomfortable when showing male-typed, i.e., stereotype-inconsistent, behavior to selection committees or in their daily work (e.g., determination or competitiveness; Heilman, 2001; Rudman et al., 2012). We investigate how heuristics and stereotyping contribute to the persistence of gendered arguments.

In the context of STEM professorships, we intend to illuminate how both subjective heuristics (Tversky and Kahneman, 1974; Heilman, 2012) and objectively observable signals (e.g., provided information on applicants' education or skills; Spence, 1973; Rynes, 1991; Connelly et al., 2011) influence evaluators' perceptions and thereby discussions in selection committees. It is challenging to precisely disentangle the influence of subjective heuristics and observable signals in recruitment. Clearly defined selection criteria (e.g., publication track record) which applicants can provide objective information on (e.g., in their CV or during interviews) can reduce subjectivity and stereotyping (Nieva and Gutek, 1980; Heilman, 2012). However, although criteria may be clearly defined and information cues on those criteria may be objectively observable, there can be subjective interpretation of selection criteria, applicant signals, or both (see, e.g., van den Brink and Benschop, 2012). For instance, applicants can provide information on their number of publications and emphasize their cooperativeness, while evaluators subjectively assess whether the exact publications reflect a successful publication track record and how cooperation would look like. We investigate the duality of subjective interpretation of seemingly objective criteria.

Investigating the more subjective and the more objective parts of applicant assessments, we also look at how specific signals that are objectively observable are evaluated for women vs. men. Evaluators may vary in their perception of how important a criterion (or signal) is, and this perception may be stereotyped reflecting the gendered success model. That is, we investigate whether success patterns are gendered, i.e., whether some signals may be success factors for women but not for men.

In our mixed-method research we collected qualitative as well as quantitative data from 45 tenured STEM professors in Germany. We conducted interviews and integrated a conjoint experiment. On the one hand, participating professors answered open-ended questions. On the other hand, they qualitatively and quantitatively evaluated hypothetical applicant profiles *via* completing a web-based conjoint experiment while thinking aloud. We inductively coded the interviewees' verbatim statements in response to the questions and profiles (Gioia et al., 2013; Eisenhardt et al., 2016) and identified emerging themes of gendered arguments. Moreover, we analyzed their quantitative evaluations of the profiles *via* fsQCA (fuzzy set qualitative comparative analysis; Ragin, 2008a) to identify success patterns that led to a high vs. low selection recommendation for male and female applicants.

Our research makes three main contributions to the literature. First, building on prior findings of gendered discussions of applicants for professorships (e.g., van den Brink and Benschop, 2012, 2014), we update and extend the knowledge of the persistence and mechanisms of gendered arguments. We show how gendered arguments build barriers for women's advancement, specifically into STEM professorships, which are high-status positions in male-dominated fields and therefore have a strong male stereotype (Carli et al., 2016; Dutz et al., 2022). We highlight that gendered arguments influence evaluations despite desired objectivity in applicant assessments. We delineate different forms of gendered arguments related to other-stereotyping, perceptions of applicants' self-stereotyping (Heilman, 2001; Hentschel et al., 2019), traditional social roles (Eagly, 1987; Eagly and Wood, 2012), and inclusion concerns based on "chilly climate" perceptions (e.g., Hinsley et al., 2017).

Second, we provide a more nuanced understanding how more subjective and more objective parts of applicant evaluations play together. Ensuring objective assessment and selection criteria, and relying on objectively observable information cues, has been suggested to boost gender equality, also in academic recruitment

(Heilman, 2012; Herschberg et al., 2015). To test for gender bias despite having objectively the exact same information cues given for male vs. female applicants (regarding publication records, showing willingness to cooperate, and having a network recommendation), we explore whether, in a situation in which applicants are comparable, success patterns lead to different selection recommendation for women vs. men.

Third, we show how combining analyses of responses to vignettes and interview questions, as well as think-a-loud comments, helped us to understand the full picture including more subjective and more objective parts of applicant assessments. We follow calls to look "behind the numbers" of quantitative survey ratings (Einola and Alvesson, 2021) showcasing an approach combining qualitative and quantitative data and apply both, inductive coding and fuzzy set qualitative comparative analysis (fsQCA). The logic of QCA fits the data structure of conjoint experiments and helps us understand success patterns that led to a high selection recommendation for men and women. The conjoint experiment indicates gender-independent and -dependent success patterns, which we can contextualize and interpret in light of interviewees' qualitative statements.

Theoretical background

Due to general uncertainty in selection decisions and incomplete information about applicants, evaluators use heuristics (Tversky and Kahneman, 1974) and signals (Spence, 1973; Rynes, 1991; Connelly et al., 2011) to assess applicants' suitability for a specific position. In the following, we first theoretically introduce heuristics, stereotyping, and signaling and subsequently discuss how they play out in academic selection committees.

Heuristics and stereotyping in recruitment

Heuristics explain how judgments are made in situations of uncertainty (Tversky and Kahneman, 1974). For instance, stereotypes are representativeness and similarity heuristics leading to mental "shortcuts" in applicant assessments (Tversky and Kahneman, 1974; Kunda and Thagard, 1996; Heilman, 2012). Heuristics assess the likelihood of an applicant's success in a specific job is based on the applicant's similarity to former "typical" successful job holders (Tversky and Kahneman, 1974). Due to gendered success models, requirements are likely to be perceived more stereotypically male the higher the perceived status of the work context and more stereotypically female the higher women's expected share in the work context (Cejka and Eagly, 1999; Koenig et al., 2011; Dutz et al., 2022). That is, perceived requirements across work contexts are stereotyped.

Furthermore, stereotype-based heuristics account for ascribing different attributes to men vs. women based on their gender (i.e., descriptive gender stereotypes; Heilman, 2001, 2012; Kunda and Thagard, 1996). Generally, men are likely to be ascribed stereotypical male *agency* (e.g., rational, analytical, and ambitious) and women are likely to be ascribed stereotypical female *communality* (e.g., emotional, sensitive, and modest). That way, heuristics account for *other-stereotyping*, as they fuel gender biases in how evaluators judge applicants and their fit to a job (Heilman, 1983, 2012; Hentschel et al., 2019).

Additionally, stereotype-based heuristics fuel *self-stereotyping*. Stereotypical perceptions influence individuals' self-characterizations based on their gender (Hentschel et al., 2019), and self-assessments of their fit to a gendered work context (Heilman, 1983, 2012). Therefore, women may see themselves as less agentic than men, and as less qualified or suitable for male-typed positions, such as high-status positions, particularly in male-dominated fields. In addition, to avoid social backlash, they may actively withdraw from displaying agentic traits and behaviors, such as self-promotion and power-seeking (Rudman, 1998; Moss-Racusin and Rudman, 2010; Okimoto and Brescoll, 2010).

Thus, heuristics fuel various stereotype-based biases. Most relevant in influencing evaluators' perceptions in applicant assessments are stereotyped requirements of jobs and stereotypes applied to applicants such as due to their gender. One way to reduce such gender biases is carefully assessing the actually needed (rather than stereotypical) qualifications and skills for the job, and applicants' respective attributes (Heilman, 2012). When assessment criteria are clear, evaluators can define concrete signals to look for in applicants.

Signals in recruitment

Especially in situations of incomplete information such as applicant assessments, evaluators rely on *signals* (e.g., applicant details in application materials) to infer attributes which they cannot directly observe (e.g., knowledge, skills, and abilities; Spence, 1973; Rynes, 1991; Connelly et al., 2011). For instance, they include information applicants provide in their CV (e.g., on performance outputs or qualifications for the job) or during the job interview (e.g., on their ability or willingness to work in a team), or information that others provide about applicants (e.g., former employers in reputation letters). Thus, signals serve as information cues for evaluators to form a picture of applicants. The signals evaluators observe and interpret during recruitment help decreasing stereotypical perceptions because signals provide information on the applicants' qualities overriding what is inferred from their gender. However, the future success of applicants is uncertain and, thus, the overall assessment of an applicant still requires subjective interpretation. Furthermore, although signals help to override stereotypical perceptions of applicants, stereotypes can still bias perceptions (see Nieva and Gutek, 1980; Heilman, 2012).

Although signals can foster objectivity in applicant assessments when assessment criteria (and signals to look for) are clearly defined, based on the actual requirements, and objectively

assessable, in practice, the criteria for assessment and selection are often ambiguous, fueling subjectivity and influences of heuristics (Nieva and Gutek, 1980; Heilman and Haynes, 2006; Heilman, 2012). Furthermore, even if a work context promotes clearly defined criteria and objective assessment, as it is in academia, the criteria may still be subjectively interpreted and construed differently for men and women (van den Brink and Benschop, 2012; Herschberg et al., 2015). That is, criteria and relevant signals may still be influenced by gendered success models and may be interpreted or weighted differently for men vs. women. This may be particularly true for high-status positions and male-dominated fields such as STEM professorships.

Recruitment for STEM professorships

In our research we investigate the mechanisms of heuristics, stereotyping, and signaling specifically in the context of STEM professorships. Professorships are high-status positions and male-dominated, particularly in STEM fields (van den Brink and Benschop, 2014; Carli et al., 2016; Catalyst, 2020c; GWK, 2020). Additionally, academia is a particularly interesting context to analyze gendered arguments despite desired objectivity because of high efforts for clearly defined and objectively assessable criteria, while discussions in selection committees are still gendered (e.g., van den Brink and Benschop, 2012; Herschberg et al., 2015).

Heuristics and stereotypes in recruitment for STEM professorships

Prior research provides evidence for the influence of heuristics and stereotypes in recruitment for STEM professorships. The high-status leadership positions in male-dominated fields possess a clear male stereotype influencing perceived job requirements (Cejka and Eagly, 1999; Koenig et al., 2011; Heilman, 2012; Dutz et al., 2022). A male stereotyped success model in academia is further reflected in the male-typed construction of academic "excellence," referring to scientific competence, which is – although a halo selection criterion – ambiguously defined and inherently gendered (van den Brink and Benschop, 2012). Therefore, the importance of stereotypical male applicant attributes is likely overestimated in assessments. Moreover, to "preserve" the gendered success model evaluators take into account "physical appearance, self-presentation, and perceived personality and leadership potential as valid criteria that can overrule other, more formally specified criteria" (van den Brink and Benschop, 2012, p. 9).

Applicant signals in recruitment for STEM professorships

One unquestionable assessment criterion in recruitment for professorships is the publication track record (see, e.g., Bedeian, 2014). Nevertheless, the actual requirements are more diverse (e.g., Eagly and Carli, 2003; Braun et al., 2013; Rehbock et al., 2021). For example, scientific output such as publications are most often team efforts; that is, cooperativeness, a stereotypical female quality (Heilman, 2012), is most likely an integral part of past and future achievements (Rehbock et al., 2021). Moreover, visibility and a good reputation in the scientific network likely help applicants (van den Brink and Benschop, 2014), while networking covers stereotypical male (e.g., impression management; Rudman, 1998) as well as stereotypical female aspects (e.g., interpersonal skills; Heilman, 2012; Gazdag et al., 2022). Thus, core evaluation criteria likely include publications, the willingness to cooperate, and having a strong network. Importantly, those criteria, despite being potentially gendered somewhat intangible, can be pre-defined and respective signals can be explicitly expressed by/for one applicant but not by/for another.

Publications are usually a crucial and formalized selection criterion (Herschberg et al., 2015). They signal scientific competence, and therefore – based on quality indicators such as journal impact factors and citations and on quantity – can be an indicator of research success that is objectively assessable. Although evaluating publications may also entail subjective elements (e.g., evaluating publications by reading them; Herschberg et al., 2015), decisions on applicants likely get more complicated – and more subjective – when applicants cannot be clearly distinguished by looking at their publications. When anticipating applicants' (future) research success and thereby their potential (e.g., for more junior researchers), due to heuristics and stereotypes it is likely that evaluators underrate the potential of minority applicants (e.g., women in STEM; Norton et al., 2004; Uhlmann and Cohen, 2005; Heilman, 2012; van den Brink and Benschop, 2012).

Additionally, *willingness to cooperate*, in general or on specific research projects, is likely crucial (Rehbock et al., 2021). While in practice difficult to assess and anticipate in applicants, applicants can emphasize their willingness to cooperate during the recruitment process. Applicants can express their willingness to cooperate by showing that they are informed and intend engagement with prospective faculty colleagues in the hiring university. Furthermore, cooperativeness as a core competency for generating scientific output in teams is likely seen as beneficial in view of future shared achievements as well as shared responsibilities among faculty members, such as academic administration tasks (Herschberg et al., 2015; Rehbock et al., 2021). Thus, cooperativeness can also be judged from how applicants describe their previous collaborations.

Furthermore, *network recommendations* can be beneficial for applicants. Network effects include higher visibility and reputation due to being part of a powerful network, which is a desirable characteristic in applicants (van den Brink and Benschop, 2014; Herschberg et al., 2015). Particularly in academia, "gatekeepers" dominate professional networks and make recruitment decisions (e.g., professors or deans, most often male), having a lot of influence and "the power of inclusion and exclusion" (van den Brink and Benschop, 2014; p. 1). Women are underrepresented in these networks and, therefore, less visible (van den Brink and

Benschop, 2014). Nevertheless, whether or not someone in the applicant's network expressed a recommendation for the applicant can be observed objectively.

Importantly, in STEM networks and also in STEM departments, there is a "chilly climate" for women (Hinsley et al., 2017; Casad et al., 2021). It is more difficult for women to operate in these contexts, due to stereotype biases (e.g., being perceived as "undeserving"; McKinnon and O'Connell, 2020), sexism, and structures mostly made for men (e.g., in regards to (low) family or care related support; Greider et al., 2019; Casad et al., 2021). Moreover, gatekeepers seem to reason that social interactions are more complicated with women in "manly" work climates (van den Brink and Benschop, 2014), using chilly climate arguments to "protect" women from entering the field or higher positions, rather than making efforts to climate or culture change and successful inclusion (see, e.g., Roberson, 2006; Mor Barak, 2015). Although this may be meant well for women, it often is an additional barrier.

Concluding, there are both subjective heuristics and objectively observable signals influencing evaluators' perceptions and discussion of applicants for STEM professorships. We investigate how heuristics and stereotyping contribute to the persistence of gendered arguments in applicant assessments in these contexts illuminating the duality of subjective interpretation of seemingly objective criteria. We further test for gender bias despite having objectively the same information cues for male and female applicants (regarding publication records, showing willingness to cooperate, and having a network recommendation); we explore whether, in a situation in which applicants are comparable, success patterns are gendered, i.e., whether signals lead to different selection recommendation for men and women.

Materials and methods

To investigate gendered arguments and gendered success patterns in applicant assessments for STEM professorships, we implemented a mixed methods approach including 45 qualitative interviews that incorporated a conjoint experiment. The interviews comprised open-ended questions that we analyzed qualitatively as well as reactions to vignettes that we analyzed qualitatively and quantitatively. The interviewees quantitatively rated hypothetical applicant profiles, while thinking aloud, commenting on their evaluations and thoughts behind their ratings (see also Einola and Alvesson, 2021). The vignettes were introduced to stimulate their thoughts on specific applicant profiles and to investigate evaluations of male vs. female applicants based on comparable applicant profiles. Capturing interviewees' answers to our questions and their evaluations of hypothetical applicants, we could analyze gendered arguments in appointment committees. Additionally, based on quantitative ratings of hypothetical applicants, we could examine success patterns for male vs. female applicants.

Research context

Our research context, i.e., the German academic system, is characterized by a lack of permanent positions, posing particular challenges for young scientists (Brechelmacher et al., 2015). For instance in 2020, there were 49,293 professors in Germany (Destatis, 2021). Per year, about 30,000 PhD students are graduating and *ca*. 33%, and another undecided *ca*. 35%, are potentially striving for a professorship that becomes vacant (Nacaps, 2021), e.g., due to professors retiring (in 2021 *ca*. 2,6%; Destatis, 2021; Zeitler, 2021). An approximate calculation of the probability of PhDs becoming professors results in 7% in mathematics/natural sciences and 20% in engineering (Krempkow, 2017). Illustrating the career time span, the average age at PhD completion was about 30 in 2020 (Destatis, 2021), and the average age of being appointed to a permanent position is still above 40 (KBWN, 2021; Zeitler, 2021). Full professors typically hold permanent positions, most often holding an own "chair" including leadership responsibility (Muller-Camen and Salzgeber, 2005; Braun et al., 2013). Due to the far-reaching nature of lifetime appointment, appointment decisions are "high-risk decisions" under uncertainty (Tversky and Kahneman, 1974; van den Brink and Benschop, 2014).

Research sample

The decisions on professorial appointments are made in appointment committees. Professors regularly take part and lead the discussions on applicants in those committees (van den Brink and Benschop, 2014; Frey et al., 2015). In their disciplines, they are "gatekeepers" in recruitment for professors-to-be and of respective academic (social and career) networks (van den Brink and Benschop, 2014). We applied purposive sampling (Patton, 2002) and intended to recruit interview partners able to share rich information on discussions in appointment committees for STEM professorships. Thus, we recruited tenured STEM professors attending appointment committees as our interviewees, balancing their mean age to avoid age bias. We recruited the professors *via* e-mail, asking them for a 30–45-min-interview on success factors of academic careers in STEM disciplines. The interviews were taken over the phone, and the interviewees could fill out the anonymized conjoint experiment survey online. Once new interviews did not lead to the identification of new major themes, we concluded sampling, based on principles of theoretical saturation (Strauss and Corbin, 1998; Gioia et al., 2013).

Finally, we included 45 tenured professors across different STEM disciplines and across different universities all over Germany. Although these positions overall are male-dominated (women currently make up for about 20% of job holders; GWK, 2020), we aimed to interview a similar number of male and female professors (51% female, M_{age} = 46.4 years), to account for both perspectives on applicant evaluations and discussions in

appointment committees. Table 1 presents participant demographics, whereby the interview partners are presented in different order (arranged by gender) than in-text to guarantee anonymity.

TABLE 1 Sample description.

Gender	STEM discipline
Male	Informatics
Male	Informatics
Male	Electrical engineering
Male	Informatics
Male	Mathematics
Male	Physics
Male	Mathematics
Male	Physics
Male	Physics
Male	Physics
Male	Informatics
Male	Electrical engineering
Male	Informatics
Male	Physics
Male	Electrical engineering
Male	N/a
Male	Mathematics
Male	Physics
Male	Informatics/mathematics
Male	Mathematics
Male	Mathematics
Male	Mathematics
Female	Physics
Female	Informatics
Female	Mechanical engineering
Female	Mathematics
Female	Mathematics
Female	Informatics
Female	N/a
Female	Product engineering
Female	Georesources
Female	Informatics
Female	Mechanical engineering
Female	Physics
Female	Mathematics
Female	Mathematics
Female	Mathematics
Female	Mathematics
Female	Sustainability
Female	Mathematics
Female	Informatics
Female	Electrical engineering
Female	Physics
Female	Physics
Female	Physics

Participants were 45 STEM professors in Germany. N/a indicates that participants did not want to indicate their discipline for the statistic.

Research design and procedure

Interview guideline and questions

We conducted semi-structured interviews based on an interview guideline with pre-defined questions, while allowing to flexibly adapt to the individual conversations (e.g., by asking follow-up questions; see Myers, 2020). The first part of the guideline covered general questions on success factors and barriers for professorial applicants in STEM (e.g., "In your opinion, what are the three most important success factors for being appointed as a professor in your field?"). Then, we presented the interviewees with vignettes showing hypothetical male and female applicants which they evaluated, (1) *qualitatively* by commenting on their evaluation of applicants and (2) *quantitatively* by rating them with respect to selection recommendation (details below). Subsequently, proceeding with the interview guideline, the interviewees were asked more specific open-ended questions on success factors and barriers specifically for female applicants as well as on how gender, other demographics (e.g., age), and family obligations are a matter of discussion in appointment committees (e.g., "Do you see specific success factors for women to be appointed as a professor in your field?" and "How was gender a matter of discussion in appointment committees you were part of?").

Vignettes and conjoint experiment

The vignettes depicting hypothetical applicant profiles construed an assessment scenario, that is, a hypothetical scenario of an appointment committee for the selection of a STEM professor. The interviewees were asked to imagine to be part of the appointment committee (as they have been in "real-world" appointment committees). Sixteen different vignettes represented 16 profiles of "shortlisted" applicants.

The 16 applicant profiles enabled a metric conjoint experiment with multiple applicant attributes varying across profiles. On the one hand, the profiles stimulated the interviewees' thoughts on applicants and the different attributes ("think aloud" evaluation; Einola and Alvesson, 2021). On the other hand, this setup tested the attributes' influence on interviewees' selection recommendation, which they indicated by a quantitative rating. Conjoint experiments are particularly useful to model (assessment) decisions (Domurath and Patzelt, 2016; Warnick et al., 2018). They allow to test for the influence of several attributes simultaneously especially regarding attribute combinations thereby exceeding the explanatory power of traditional experiments. Varied attributes, in our case of construed applicant profiles, present the independent variables in conjoint experiments, while the (quantitative) assessments, in our case the selection recommendation for the applicants, comprise the dependent variable (Domurath and Patzelt, 2016; see also Green et al., 2001). In the applicant profiles, we varied four attributes with two levels each in a fully-crossed within-design ($2^4 = 2 \times 2 \times 2 \times 2 = 16$ different combinations, i.e.,

profiles). Interviewees assessed all possible combinations of attributes in applicant profiles. The varied attributes and their levels were publications (solid vs. outstanding), willingness to cooperate (low vs. high), network recommendation (non-present vs. present), and applicant gender (male vs. female).

Publications, meaning the quality and quantity of applicants' publications, was included as the most explicit factor or criterion representing scientific competence and amenable for objective assessment (while there are still varying and biased arguments of how and which publications are taken as cues for scientific competence; see, e.g., van den Brink and Benschop, 2012). The vignettes either stated that the applicant has *solid* publications (i.e., meeting but not exceeding average expectations) or *outstanding* publications (i.e., exceeding average expectations).

Willingness to cooperate, meaning applicants' signaled interest in cooperating with prospective faculty or university colleagues, was included as the second relevant factor in appointment decisions, although less suitable for objective assessment (see, e.g., van den Brink and Benschop, 2012, 2014). Without relevant and unbiased "proof" (such as knowledge of previous collaborations), this may be a factor subjectively discussed in appointment committees, based on impressions of applicants, their conveyed personality, interests, and appearance in formal (and informal) talks. Levels were *low* or *high* willingness to cooperate.

Network recommendation, meaning that the applicant is recommended in some committee member's personal (research) network, was another potential success factor in our analysis. Network recommendations play a crucial role in appointment decisions, informally discussed rather than as formal criteria, and are likely more common for male than female applicants, especially in STEM fields (van den Brink and Benschop, 2012, 2014). Levels we compared were *non-present* (i.e., there is no present/known recommendation for the applicant) and *present* (i.e., there was present/shared a positive network recommendation for the applicant).

Applicant gender was varied assessing whether thoughts and evaluations differed based on applicant gender. The levels were *male* and *female* indicated by a blurred image/icon of a male or female face and the indication of Mr. or Ms. in the profiles.

In their assessments, the interviewees were to assume that the applicants essentially differ in regards to the four varied attributes on the profiles. In the interviews, we assessed whether publications, willingness to cooperate, and network recommendation were seen as important and realistic selection criteria (and, thus, reasonable to be selected as conjoint experiment decision criteria; see Warnick et al., 2018). The attributes were evaluated realistic and important selection criteria, whereby publications and willingness to cooperate where often seen as "showstopper" criteria [e.g., Interview (Int.) 26(male)] and network recommendations were evaluated more controversially. A few interviewees highlighted that the latter should not be influencing selection decisions, while others emphasized that those (still) have crucial influence in discussions about applicants, especially when applicants' documents do not allow for clear judgment of their suitability (e.g., Int. 10(female)).

To obtain a quantitative measure of the dependent variable, the participants indicated for each applicant profile their selection recommendation, on a 1-item 7-point Likert scale ("Please indicate based on the profile information: Would you advocate for this person to be selected for the list of applicants that are considered further?"; 1, "no, definitely not" to 7, "yes, definitely"), modified from Heilman and Okimoto (2008). To test for test–retest reliability of the interviewees' quantitative ratings on this measure, we randomly replicated four out of the 16 profiles on each participant (Warnick et al., 2018). We also included a practice profile to familiarize participants with the setting (such that, in total, the interviewees rated 21 profiles; Warnick et al., 2018). Both, the replication profiles as well as practice profile, were not included in the main analysis (Aiman-Smith et al., 2002; Warnick et al., 2018). The conjoint experiment survey ended with a demographic survey.

Data analysis

Inductive coding and visualization of emerging themes

We analyzed the qualitative data of the STEM professors (i.e., their verbal answers to open-ended questions and verbal statements on hypothetical applicant profiles) by means of qualitative, inductive coding (Gioia et al., 2013; Eisenhardt et al., 2016). In addition, in our data analysis process, we discussed different visualizations of the emerging themes (Miles and Huberman, 1994).

Following the inductive analysis procedure suggested by Gioia et al. (2013), we initially applied a *first order analysis* of categories arising from the data (see also Strauss and Corbin, 1998). Thus, we initially closely adhered to the subjects' verbal statements and not yet formed (theoretical) higher-order categories, allowing a large number of parallel first order categories to emerge from the analysis. Those codes captured statements in which participants outlined their view on how appointment committees treat women differently than men, which behaviors they observed in male and female applicants, and how they evaluate participants regarding specific criteria including publications, cooperation, and networks.

In a second step, we applied a *second order analysis* looking for similarities and differences between the initial categories. Thereby, we identified "whether the emerging themes suggest concepts that might help us describe and explain the phenomena we are observing" (Gioia et al., 2013, p. 20). In doing so, we went back and forth between data-based codes and theoretical level themes. We focused on those emerging themes that are of particular interest as they offer new theoretical insights (Corley and Gioia, 2004; Gioia et al., 2013). For example, on themes that indicate how women are perceived as "extraordinary" or particularly salient questioning of female applicants in appointment committee discussions.

Third, we further distilled our second order themes to *aggregate dimensions* towards a more abstract and interpretative, theoretical view (Gioia et al., 2013). In the findings section, we present our data structure, explaining how we went from the original data to our theoretically aggregated dimensions (Corley and Gioia, 2004; Gioia et al., 2013). For example, we grouped codes referring to perceived self-questioning of women and those referring to evaluators questioning similar attributes in women (abilities, general traits, commitment).

FsQCA of quantitative data

To analyze STEM professors' quantitative ratings (i.e., the quantitative scores they indicated for the different vignettes of hypothetical applicants), we performed a fuzzy-set qualitative comparative analysis (fsQCA; Ragin, 2008a).

The logic of QCA is to identify combinations or *configurations* of factors that indicate a specific outcome of interest (Ragin, 2008b; Pappas and Woodside, 2021), whereby the analysis allows to capture "multiple paths that lead to the same outcome" (Pappas et al., 2020; p. 5). Therefore, applying QCA, we used a configurational approach (Delery and Doty, 1996; Fiss, 2007), investigating configurations of theory-based, manipulated attributes (their presence or absence, respectively) that lead to a specific outcome, rather than a variance-based approach focusing on attributes' isolated effects (Pappas and Woodside, 2021). As our outcome variable was measured on a 7-point Likert scale (i.e., non-binary), we performed a particular type of QCA, i.e., fuzzy-set QCA (Ragin, 2008b; Pappas and Woodside, 2021). Enabling higher complexity of variable levels (Ragin, 2000; Rihoux and Ragin, 2008), fsQCA is a popular variation of QCA to analyze quantitative data (Pappas and Woodside, 2021), increasingly used in business and management (Kumar et al., 2022), entrepreneurship, and innovation research (Kraus et al., 2018).

We used fsQCA to analyze which configurations of the manipulated attributes on hypothetical applicant profiles led to a high selection recommendation, including applicant gender and, additionally, evaluator (i.e., interviewee) gender in configurations. To do so, we analyzed all possible combinations of factors to predict the outcome of high compared to low selection recommendations (Woodside, 2013, 2016; Pappas and Woodside, 2021) based on fsQCA software (3rd version; Ragin and Davey, 2016).

First, we employed *data calibration* (Ragin, 2008a; Pappas and Woodside, 2021) converting our non-binary outcome variable "selection recommendation" into degrees of membership of 0 to 1 by setting three anchor points: full membership, crossover point, and full non-membership. Full membership referred to "high selection recommendation" and full non-membership to "no high selection recommendation" or "low selection recommendation"; the cross-over point indicated "the value where there is maximum ambiguity as to whether a case is more in or more out of the target set" (Pappas and Woodside, 2021; p. 8). The three anchor points were set at 6, 4, and 2, as suggested for 7-point Likert scales (Ordanini et al., 2014; Pappas et al., 2016).[1] We did not calibrate the variables for the manipulated attributes on hypothetical applicant profiles, nor evaluator gender, due to their already binary levels.

Second, we generated a *truth table* (Ragin, 2008a; Pappas and Woodside, 2021). The truth table in fsQCA displays all possible configurations of factors (in our case of the manipulated attributes in the conjoint experiment design, i.e., publications, willingness to cooperate, network recommendation, applicant gender; as well as evaluator gender). As the attributes and evaluator gender had two levels each, the truth table showed 32 different configurations ($2^5 = 32$ combinations). The truth table shows the frequency for each possible configuration (Pappas and Woodside, 2021). As in our conjoint experiment every participant rated all vignettes/applicant profiles, thereby all possible configurations of attribute levels, the frequency for each configuration was largely fixed by the number of participants; only the frequency for configurations with evaluator gender varied as we had 23 female and 22 male participants.[2] The truth table also shows the configurations' consistency, where we set the recommended thresholds for "raw consistency" at minimum 0.75 (Rihoux and Ragin, 2008) and for "proportional reduction in inconsistency" at 0.7 (Greckhamer et al., 2018; Pappas and Woodside, 2021).

In a third step, we proceeded with *obtaining the configurations* (or "solutions"), setting the individual factors as being "present or absent" in the configurations (Ragin, 2008a; Pappas and Woodside, 2021). For high selection recommendations, the analysis yielded three different configurations; for low selection recommendations, the analysis yielded two different configurations. We further examined what are core or peripheral conditions in the obtained configurations by comparing the intermediate and parsimonious solutions identified (Pappas and Woodside, 2021; Fiss, 2011).

Empirical findings

Qualitative data

In the following, we present the results of our inductive coding of STEM professors' qualitative, verbatim statements to open-ended questions and hypothetical applicant profiles. The abbreviations "m" and "f" indicate the gender of interview partners as male or female.

1 To avoid a dropout of conditions exactly at 0.5, we added a constant of 0.001 to conditions <1, in our data set (Ragin, 2008b; Fiss, 2011; Pappas and Woodside, 2021).

2 Therefore, we did not set a frequency threshold to include or exclude cases (see Ragin, 2008a; Fiss, 2011).

General subjectivity in applicant assessments

Interview statements highlighted the general subjectivity in discussions of applicants in appointment committees. As explained by one of the professors (Int. 20 (m)), "[while] appointment processes are quite objectivized on paper, in reality, they develop their own dynamics that do not necessarily make them as objective as they seem." Other professors emphasized their perception of "subjectivity" in applicant discussions (e.g., Int. 27(m), 29(f)). One interviewee (10, f) specified that "occasionally, when the documents do not allow definite judgment, it only takes a few words to suddenly push a certain applicant." While the professors mentioned some explicit criteria for assessment and selection (such as publications, e.g., Int. 9(m), 13(m), 20(m), 26(m), 44(f)), they repeatedly highlighted that discussions in appointment committees often gain momentum in unpredictable directions (also Int. 13(m), 15(m), 19(f), 37(m)).

Gendered arguments in applicant assessments

Interview statements further highlighted that applicants' gender is an issue explicitly or implicitly in appointment committee discussions, reflected in different types of gendered arguments (Figure 1).

Women's exceptional status

Among the professors there seemed to be a consensus that women as applicants for STEM professorships have an exceptional status; however, while some professors were arguing for a *perceived female advantage* due to women's exceptional status, other statements pointed to *femininity as deviance due to outgroup derogation*.

Perceived female advantage

Some professors described an "advantage" of female applicants standing out due to their gender, arguing that, in appointment committees, female applicants' profiles are always looked at and discussed in more detail. For example, Interviewee 24(m) stated:

> "You can be pretty sure to not be overlooked [as a female applicant for a STEM professorship]; you still need to be good, but if you are, you don't need much luck […]. If this is reflected in two objective criteria: publications and visibility–that you are perceived to be good–then, you almost surely find a suitable position."

More generally, Interviewee 1(m) argued that women in STEM enjoy more support and encouragement than men in STEM such as when describing that "everyone wants women to do technical staff […]; and they literally bring out the red carpet for women." Interviewee 27(m) sees "women are privileged [in appointment decisions] but only to certain extent–when substantiated by professional qualification." Interestingly however, some interviewees say that even if they prefer women, sometimes they have difficulties to argue for them, such as Interviewee 12(m): "There are always a lot of top candidates–and I am preferring females; but the majority would prefer males and that's why there are hardly any women." Other interviewees perceive the female advantage even clearer, for example Interviewee 34(m) stated "with the same criteria met, female applicants are preferred." Thus, interview statements indicate that women might have an advantage in some situations.

Femininity as deviance due to outgroup derogation

Other interview statements rather point to femininity as deviance to a male stereotyped template of selecting applicants. "You have a problem if you don't fit the frame–brutally speaking, somehow, if you are not the big alpha male," explained one of the professors (Int. 12(m)). Another professor (Int. 4(f)) described: "Specific types of CVs are favored–which are statistically more found in men," and Interviewee 29(f) specified that there is little tolerance for female-typed careers:

> "The actual understanding of the situation and of careers that are not perfectly linear and do not follow the typical pattern of a male career but may have interruptions or deviations–for such unusual biographies, there is no high tolerance in committees."

In line with this logic were arguments assigning women an outgroup status, for example in professional networks. For instance, Interviewee 43(m) argued, "I can imagine–since men still dominate the field–that it might be easier for them to be recommended within their network." Another professor (Int. 37(m)) explained "a lot of socializing at workshops or conferences takes place over a beer in the evenings–at this point, women are most often already gone." Thus, being female is seen as deviance, and women are perceived to be less likely integrated in the network, such that they often end up as "outgroup."

Questioning of women

In addition to arguments with respect to women's exceptional status, we observed that there was a lot of questioning of female applicants in the statements of our interviewees. We observed three kinds of questioning categories, i.e., questioning ability, general traits, and commitment.

Questioning ability

Statements of interviewees pointed to questioning of women's ability. Outlining that the ability is questioned, one of the professors (Int. 45(f)) described:

> "With women it is often assumed that a job might be too big for them, too difficult, too early. This shows that gender is discussed. It is not discussed in a gender-neutral way, although

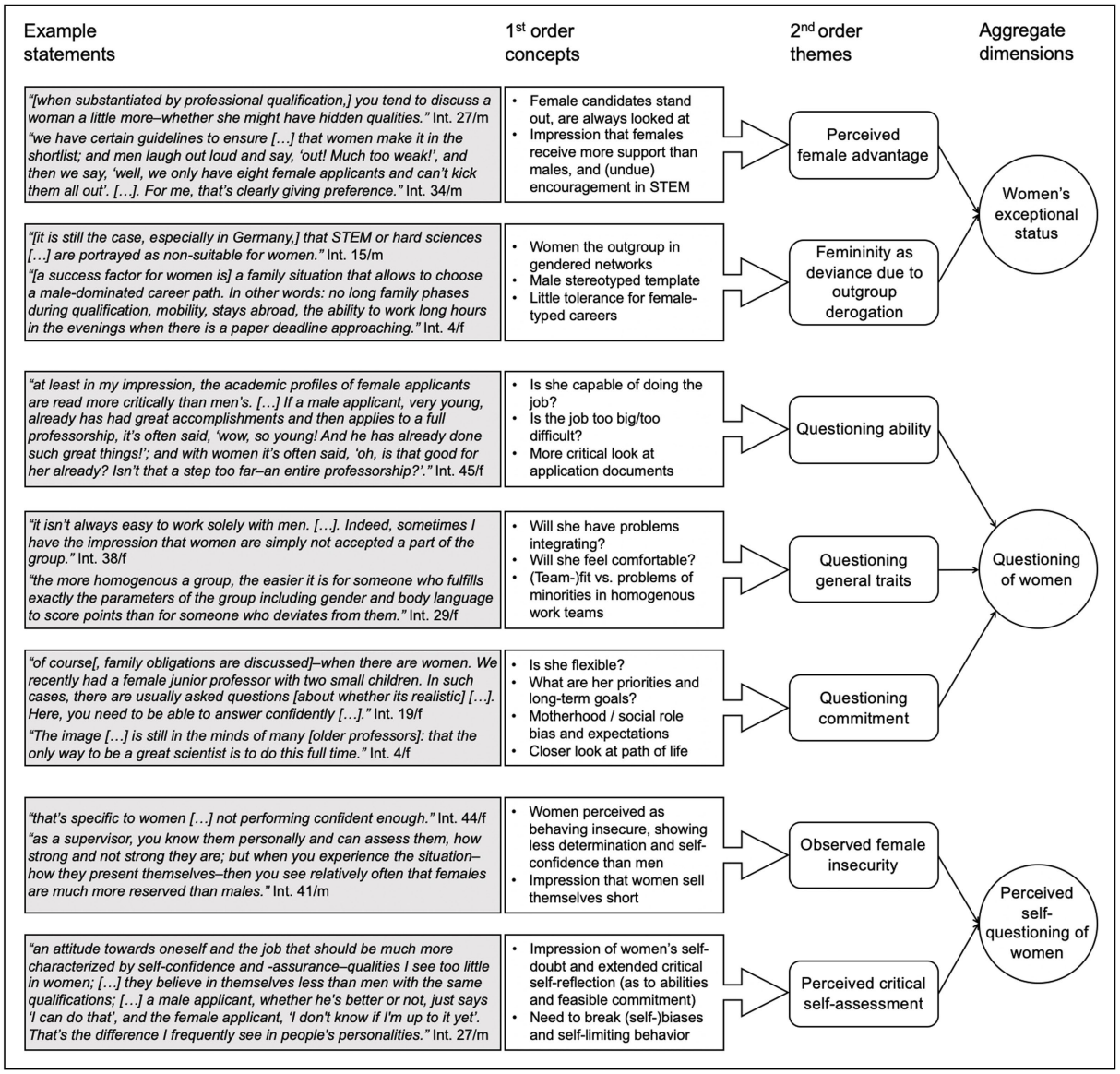

FIGURE 1
Data structure of inductive coding of STEM professors' qualitative, verbatim statements [according to Gioia et al. (2013)]. "m" and "f" indicate the gender of interview partners as male or female.

> we all claim for ourselves that we are super neutral and not biased; that is simply not true."

Another professor (Int. 35(f)) framed it differently: "My impression is often that women have to be slightly better than comparable men; because women are taken a more critical look at." Both statements point to preconceived notions of female applicants' potential insufficient ability, respectively to (prior) skepticism of whether female applicants are able to handle the job of a STEM professor. Interviewee 14(m) reported questioning in a more explicit form: "In engineering commissions, I often witnessed openly expressed bias: Can *women* even do the job?," while referring to reactions of older committee members in particular. Additionally, interviewee statements reflect stereotypical thinking patterns in abilities needed:

> "Some soft skills may not be valued sufficiently–because factors such as 'women's groups work better and women create a better group atmosphere', what you hear often, are hardly considered in appointments […]. In this regard, I can imagine that certain qualities of women are undervalued." (Int. 24(m))

Another professor (Int. 13(m)) emphasized the need of "trying to get away from STEM being somehow more masculine and social professions more feminine," connecting to gender-stereotypical

ability requirements across (male- vs. female-dominated) domains. Thus, we could observe salient (though often implicit) scrutinizing of female applicants' (general) ability for the jobs, including references that a more critical look is taken at their ability.

Questioning general traits

The professors' statements also pointed to questioning of whether women's traits fit the male-dominated environments and groups. Under this category, we summarized statements referring to considerations of (team-)fit (as female minority and "rare bird" among male colleagues; Int. 6(m)), and whether women will have problems integrating or will feel uncomfortable due to (women's vs. men's) alleged different character and behavioral traits and style of interacting. For instance, more generally, Interviewee 6(m) stated that "if you are in a group of 20 scientific staff members and the only women, this also has an influence on the whole group dynamic, of course." The professor further explained: "A women alone in a male-dominated group; that can cause difficulties in terms of assertiveness, discourse, etc.–there are studies on that." Another professor stated:

> "The conversational atmosphere, the way men interact–that's different from how women interact […]; you have to be able to adjust to it. You must not react too sensitive to mocking remarks or dirty jokes […]. I feel like those [women] who made it are resilient in that regard." (Int. 19(f))

More so, Interviewee 9(m) described the impression that "in a subtle, subjective way, appointment committees tend to appoint people who fit the majority of the people in the commission best." While "the conceit of what is a professor is still very present" (Int. 12(m)), women seem to be perceived as different. All those statements indicated that the fit of women regarding their general traits is questioned.

Questioning commitment

Besides questioning female applicants' ability and general traits, we found questioning of their commitment, flexibility, and whether they may have other priorities than or besides the job, while the job is assumed to require the job holder's full dedication. One of the professors explained more detailed (Int. 6(m)):

> "You are usually looking for someone who can spend a lot of time [on the job] and, of course, you don't want to put someone in the situation where he or she is overchallenged when appointed. Thus, you try to find out very precisely what the candidate's life organization looks like–even if, of course, this should not really be influencing the decision […]. However, when it comes to figuring out how likely the candidate is to accept the position and to do the job the way you think it should be done–these are rather soft criteria you cannot easily quantify. Then it is also discussed: What is the family situation like? What is the person's goal in life–generally speaking? Does it fit a science career?"

Another professor (Int. 18(f)) exemplified in regards to a female applicant: "Certainly, you think about whether they'll really come here: Once we also had a young woman with two children–single–so about how she wants to solve that." Interviewee 9(m) further explained that, in women, "especially when it comes to children, the self-confident appearance must be real; if just saying 'Yes–I will manage that' but not believing so, people will notice that." This category of statements also reflected traditional role expectations or fulfillment, generally existing or anticipated. For instance, one professor (Int. 31(f)) stated, "it's [still] rather that women are centered on their husband and their husband's careers than the other way around […]; I personally know few female colleagues where it was the case that their husbands oriented themselves to what their wife needs, obtained, or has to do [career-wise]." These and similar statements indicated the questioning of women's (general) commitment to the jobs, in regards to time and work investment.

Perceived self-questioning of women

Analyzing and aggregating the emerging themes related to gender, we further found interviewed professors reported they *observed female insecurity* in appointment processes or *perceive critical self-assessment*, particularly in women.

Observed female insecurity

This category outlines statements concerned with women's demeanor and appearance in appointment committees, specifically summarizing professors' observations or perceptions of women behaving insecure, showing less self-confidence or determination than men, in the process. One professor described:

> "It can still be observed that women behave needlessly modest and insecure. I think men often have the habit of being more self-confident, perhaps too self-confident, and women sometimes sell themselves short." (Int. 26(m))

Other professors share the observation of low or less self-confident demeanor and presentation of their achievements among women, in appointment committees (e.g., Int. 19(f), 44(f)). More directed towards showing determination in appointment committees and when describing their vision and future professional plans, one of the interviewees (Int. 23(f)) explained:

> "They [the applicants] need to have a plan of how they want to fill their subject in the future–I think, in many women, this is the biggest weakness. They signal a lot of cooperativeness; but when asked 'what do you want to do in this position in the future?', many of them have a very vague idea. Far less clear than men often do."

These observations or impressions were shared in the sense of being perceived as barriers to women's chances in appointment processes and their career advancement in general; or, in a similar

fashion, as recommendations for female applicants in particular. For instance, Interviewee 3(f) recommended:

> "[I would recommend to women] to not be shy–somehow, to assert yourself a bit and clearly state: 'I did that'; because often I have the feeling that women do that less often. For example, when there is a project that was done in collaboration with others, to clearly say: 'Yes, I did that'; because I think women tend to take a back seat."

Thus, especially in female applicants, professors seem to observe insecurity in their behavior and appearance, when they are presenting themselves to be appointed as professors.

Perceived critical self-assessment

Another theme pointing to perceived self-questioning of women emerging from the data was perceived critical self-assessment, particularly in women. In this category, we clustered statements that point to a general impression of women in STEM academia having high levels of self-doubt and engaging in extended critical self-reflection; thus, outlining a general bias participating professors see in women's perception or belief about themselves and their own abilities. For instance, Interviewee 41(m) described the following impression:

> "The average female candidate on her career path has more self-doubt and self-criticism, and also expresses them openly. While the typical 'male STEM' is a star–at least he thinks he is."

Another professor (Int. 19(f)) described that self-questioning is even a good feature in science careers but at the same time one needs to be self-assured when pursuing a professorship:

> "Women are more covered in doubt. In science, I believe self-questioning is even a good feature–but pursuing a professorship […] a self-assured manner is key to be seen and perceived as positive and successful."

Additionally, interviewees described the situation of pursuing a STEM professorship in Germany. They emphasized high uncertainty because of non-permanent contracts and high mobility demands including regular changes of location until appointed as a professor as potentially arousing more doubt in female than male scientists in striving to reconcile work and family (e.g., Int. 20(m), 24(m), 31(f), 33(f), 34(m), 35(f)). All those statements indicated that professors see a particularly critical self-assessment, including high self-doubt, as a barrier in female scientists and applicants for STEM professorships.

Interplay of gendered arguments

In discussions of applicants the gendered arguments are unlikely to be clearly separated (e.g., general traits may be interpreted as abilities) and reciprocally bias arguments. Building on our findings, Figure 2 illustrates how the male-dominated context (triangle on the top) and the gender "atypical" career of female applicants (triangle on the bottom) shape women's exceptional status and the perceived self-questioning of women which may in turn fuel the questioning of women (arrows towards the questioning circle) stemming from questioning their fit regarding ability, general traits, and/or commitment.

Quantitative data

Besides analyzing STEM professors' qualitative verbatim statements, we explored their quantitative ratings of hypothetical applicants in a fsQCA. We explored how combinations of different applicant success factors (their publications, willingness to cooperate, and network recommendation) and demographics (applicant gender as well as evaluator, i.e., interviewee, gender) led to high vs. low selection recommendations for hypothetical applicants.

We found three configurations (consistency cutoff at 0.755) associated with *high selection recommendations*, presented in Table 2. Configuration 1 of the present core conditions *outstanding* publications and *high* willingness to cooperate led to high selection

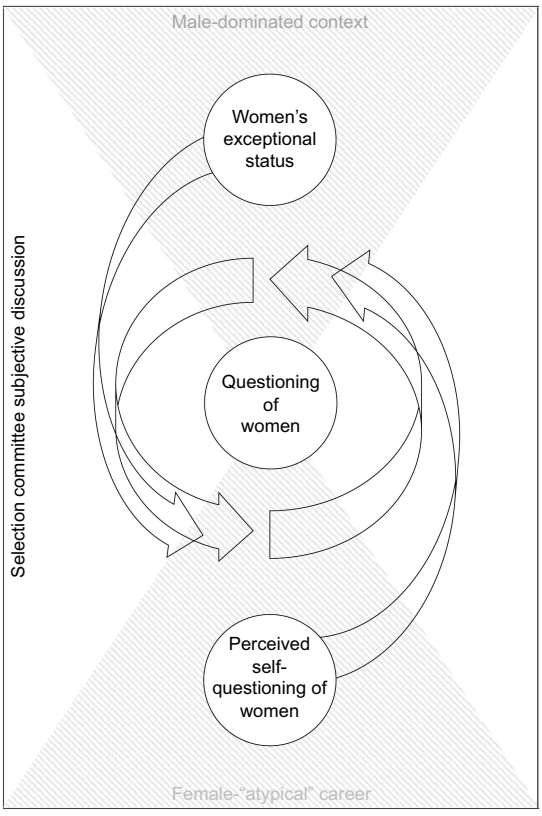

FIGURE 2
Selection committee subjective discussion of female applicants for STEM professorships (model based on 45 interviews with STEM professors in Germany).

TABLE 2 Configurations leading to high selection recommendation.

	Configuration		
	1	2	3
Success factors			
Publications	●		
Willingness to cooperate	●	●	●
Network recommendation		●	●
Demographics			
Applicant gender		●	
Evaluator gender			●
Consistency	0.976	0.878	0.878
Raw coverage	0.414	0.186	0.191
Unique coverage	0.256	0.039	0.041
Overall consistency: 0.918			
Overall coverage: 0.537			

Black circles indicate the presence of a condition (i.e., publications *outstanding*, willingness to cooperate *high*, network recommendation *present*, applicant gender *female*, and/or evaluator gender *female*). All conditions are core conditions. Blank space indicates a "don't care" condition.

TABLE 3 Configurations leading to low selection recommendation.

	Configuration	
	1	2
Success factors		
Publications	⊗	⊗
Willingness to cooperate	⊗	⊗
Network recommendation		⊗
Demographics		
Applicant gender		
Evaluator gender	⊗	
Consistency	0.906	0.906
Raw coverage	0.270	0.275
Unique coverage	0.129	0.134
Overall consistency: 0.892		
Overall coverage: 0.404		

Circles with "x" indicate the absence of a condition (i.e., publications *solid*, willingness to cooperate *low*, network recommendation *non-present*, applicant gender *male*, and/or evaluator gender *male*). All conditions are core conditions. Blank space indicates a "don't care" condition.

recommendations, regardless of whether there was a network recommendation, applicant gender, and evaluator gender. Configuration 1 was the configuration associated with high selection recommendations with the highest consistency and coverage. Additionally, configuration 2 of the present core conditions of a *female applicant*, a *high* willingness to cooperate, and a *present* network recommendation led to high selection recommendations, and then whether publications were solid or outstanding and evaluator gender did not matter. Moreover, configuration 3 of the present core conditions *female evaluator*, a *high* willingness to cooperate, and a *present* network recommendation led to high selection recommendations, and here applicant gender and whether the applicant had solid or outstanding publications did not matter. Accordingly, we found one configuration that led to high selection recommendations independent of gender (configuration 1), one configuration that requires female applicant gender (configuration 2), and one configuration that requires female evaluator gender (configuration 3). This indicates that publications and the willingness to cooperate are general success factors, a network recommendation may become important for female applicants, and female evaluators seem to care about a network recommendation.

We found two configurations (consistency cutoff at 0.892) associated with *low selection recommendations*, presented in Table 3. The configurations indicate that applicants received low selection recommendations when some core conditions were *absent*. The first configuration (configuration 1 in Table 3) showed that, with a *male evaluator*, *solid* (i.e., not outstanding) publications and *low* (i.e., not high) willingness to cooperate led to low selection recommendations, regardless of whether there was a network recommendation and of applicant gender. The second configuration (configuration 2 in Table 3), with similar consistency and coverage, showed a combination of *solid* publications, *low* willingness to cooperate, and *no* present network recommendation led to low selection recommendations, and here neither applicant gender nor evaluator gender mattered. Accordingly, the first configuration was dependent on evaluator gender and the second configuration led to low selection recommendations independent of gender (applicant and evaluator gender). Those findings indicate that all three success factors (i.e., publications, willingness to cooperate, network recommendation) were taken somewhat into consideration and a network recommendation does not seem to matter for male evaluators in our study.

Discussion

Shedding light on the subjective interpretation of seemingly objective selection criteria, the aim of this research was to investigate gendered arguments in applicant assessments for STEM professorships. The recruitment contexts promote clearly defined criteria and objective assessment; still, the criteria can be subjectively interpreted and construed differently for men vs. women, leading to gender-biased evaluations (van den Brink and Benschop, 2012; Herschberg et al., 2015). In our research, we illuminate both the influence of subjective heuristics and objectively observable signals in applicant assessments. To test for gender bias despite having objectively the same information cues given for male and female applicants, we explored whether success patterns are gendered.

Our findings indicate several types of gendered arguments which are likely to fuel each other and fuel gendered discussions in appointment committees for STEM professorships. Those include arguments regarding women's exceptional status,

questioning women, and perceived self-questioning of women. Additionally, in a situation in which applicants are comparable regarding publication records, showing willingness to cooperate, and having a network recommendation, we found both gender-independent and gender-dependent success patterns (i.e., "configurations" in fsQCA) for selection recommendation.

Gendered arguments fueling gendered discussions

Previous research revealed gendered discussions based on a "proven masculine success model" in appointment committees for professorships (van den Brink and Benschop, 2012, 2014, p. 14). Focusing on STEM professorships, which are particularly male stereotyped high-status positions in academia (Carli et al., 2016; Dutz et al., 2022), our findings highlight different forms of gendered arguments despite desired objectivity in applicant assessments; thereby updating and extending our knowledge of the persistence and mechanisms of gendered arguments in appointment committee discussions.

Gendered arguments revealed a paradox of women's exceptional status in the contexts. Female applicants for STEM professorships seem to be perceived as having a "unique selling point" in recruitment processes (i.e., their gender). However, until they get to the point where gender is perceived to help them get a position, their exceptional status and gender was related to adverse deviance with the male "prototype" of STEM professors and outgroup derogation. The perceptions emphasize, on the one hand, women's "exceptional" representation and, on the other hand, allegedly required "exceptional" attributes of women (e.g., being assertive "as men," following a male-typed career track without interruptions, and being visible in male-typed networks despite barriers for women; see, e.g., Heilman, 2012; van den Brink and Benschop, 2014). Thereby, our findings show arguments from evaluator perspective to support a gender authenticity challenge for women in science careers ("unusual" for their career and "unusual" for women; Faulkner, 2007), likely fueled by narratives of their exceptional status (Müller, 2021). Future research needs to consider that exceptional status arguments in discussions of female applicants are complex and may help or hinder gender equality efforts.

Furthermore, questioning women found in our study comprehensively illustrates in the context of STEM professorships how female applicants are not given the benefit of the doubt as (perceived) "risky" options (Fleming Cabrera, 2010; van den Brink and Benschop, 2014). First, in line with status characteristics theory (Foddy and Smithson, 1989; Foschi, 1992), ability questioning indicates that female applicants (as low-status group) need to prove their ability more than male applicants (as high-status group), specifically in STEM where "ability" is male-typed (see also Biernat and Kobrynowicz, 1997). This further relates to a greater potential of ascribing *female* applicants a perceived lack of fit with male-typed job requirements (Heilman, 1983, 2012). Second, general traits as relating to perceived fit, same as abilities (Kristof-Brown, 2000), were subject to questioning regarding perceptions of a "chilly" climate for women in STEM (see e.g., Casad et al., 2021). The focus of arguments was women's adaption to the climate rather than adapting the climate, presenting a defective "fix the women" solution (Burkinshaw and White, 2017). Last, although female applicants may be perceived in different light associated with the male-typed context if they are perceived as qualified (e.g., possessing male-typed abilities and traits; Eagly, 1987; Dutz et al., 2022), other prejudicial arguments related to social role perceptions, such as women's (anticipated) care role and alleged lower commitment, can still be influencing perceptions (see also Peterson Gloor et al., 2021). We call for future research to investigate how the questioning arguments influence each other and perceived applicant fit.

The questioning arguments clearly relate to heuristics and stereotyping (Tversky and Kahneman, 1974; Kunda and Thagard, 1996; Heilman, 2012). Of the different types, questioning ability is most likely to be discussed as if it would be "objective," although likely based on heuristics (Tversky and Kahneman, 1974) and gendered standards (van den Brink and Benschop, 2012; Herschberg et al., 2015). Evaluators may be particularly inclined to question general traits and commitment when the female applicant is perceived to fulfill the general requirements for the job, i.e., is "approved" in terms of evaluated abilities. Both, questioning general traits and commitment, seem to be more recognized as subjective and "informal"; the arguments unavoidably include judgment based on hypothetical considerations, and the higher the ambiguity in applicant assessments, the more likely stereotypes influence perceptions of applicants (Nieva and Gutek, 1980; Heilman, 2012).

Perceived self-questioning of women, further reflected in gendered arguments, connects to *perceived* self-stereotyping of women (Heilman, 2012; Hentschel et al., 2019), e.g., assuming that women generally think they cannot handle the job or are not good enough, therefore engaging in self-limiting behavior. On the one hand, this may indicate a gender-stereotypical image evaluators still have of female applicants (e.g., uncertain and self-critical) vs. ideal scientists (e.g., decisive and high self-regard; Carli et al., 2016). On the other hand, this may indicate a less positive self-impression of women than men in STEM careers. That is, when engaging in self-stereotyping, women may question their "unusual" career track and perceived "gender-atypical" behavior on the job, not perceiving gender authenticity (Faulkner, 2007; Müller, 2021), and thus their fit and commitment to the job (e.g., Heilman, 1983, 2012). Gender authenticity, not feeling the need to explain one's career choice (Faulkner, 2007), may enhance women's positive self-impression and reduce self-doubt. Importantly, arguments of perceived self-questioning of women again reflect a "fix the women" rather than "fix the system" approach (Burkinshaw and White, 2017). Interestingly, while self-criticism and low (demonstrated) self-confidence were seen as barriers for women applying to STEM professorships, self-criticism was generally seen as a crucial trait in scientists and being overly self-confident in

appointment processes as rather negative, challenging the stereotypical view of ideal scientists (Carli et al., 2016).

Objectively observable signals and gendered success patterns

We not only investigated gendered arguments, but also which combinations of objectively observable signals or success factors can lead to selection recommendations. Previous literature suggests that, beyond criteria directly signaling academic competence (e.g., publications), there are gender-stereotyped, notably stereotypical female, requirements (e.g., Rehbock et al., 2021). For example, expressing willingness to cooperate and being recommended in one's scientific network can be important signals of potential academic success incorporating stereotypically female components (see, e.g., Gazdag et al., 2022; Heilman, 2012). The findings of our fsQCA indicated that gender-independent success patterns for selection recommendations, with respect to both applicant and evaluator gender, include not only outstanding publications but also signaling the willingness to cooperate as success factors. Additionally, our results indicated that network recommendations, suggesting interpersonal skills that are stereotypically female (but also stereotypical male self-promotion skills; Rudman, 1998; Heilman, 2012), can make a difference for men and women alike.

Interestingly, applicants without outstanding publications (having only solid publications) were still recommended for selection, when they were either female or had a female evaluator, when they signaled willingness to cooperate and additionally had a network recommendation. Conversely, with a male evaluator, solid publications and low willingness to cooperate led to a *low* selection recommendation for male and female applicants, and here a network recommendation did not matter. Thus, a network recommendation in combination with signaling high willingness to cooperate can become particularly important for female applicants, and female evaluators seem to care about a network recommendation more than male evaluators. In other words: A network recommendation legitimizes female applicants considered to be perceived as "risky" options and female evaluators seem to be particularly aware that such recommendations are needed to be accepted in the community (see van den Brink and Benschop, 2014). However, it was also recognized in our interviews that women are often the "outgroup" to networks in STEM academia and it may be more difficult for women to get a network recommendation (see also van den Brink and Benschop, 2014). Thus, our findings point towards several obstacles but also some success factors particularly for women.

A mixed methods approach to capture complexity of gendered influences

Our findings on gendered arguments and gendered success patterns, and the subjective interpretation of seemingly objective criteria, emphasize the complexity of gendered influences in appointment committees for STEM professorships. Combining analyses of responses to vignettes and interview questions helped us to understand the more subjective and the more objective parts of applicant assessments, including interviewees' reasoning behind their survey ratings (see also Einola and Alvesson, 2021), and how applicants may be evaluated based on comparable profiles controlling for influences of gendered arguments. Taking this approach, we are able to contextualize and interpret the survey ratings in light of our interviewees' verbatim statements highlighting some interesting aspects.

Introducing the assessment scenario and vignettes, we also introduced the proposed selection criteria publications, showing willingness to cooperate, and having a network recommendation. Publication records were often mentioned as important selection criterion beforehand, while publication success was interpreted in light of a continuous track record especially female applicants sometimes may not have due to interruptions for parental leave. Cooperativeness was seen as highly crucial in hypothetical applicants, while not so much discussed before the criteria was introduced in the assessment scenario. Conversely, gendered arguments rather pointed to the fact that such qualities stereotypically more found in women are undervalued in appointment committee decisions. Last, visibility and being well-known in the scientific network were discussed as crucial even before the assessment scenario was introduced, while, in the scenario, the interviewees were tentative to incorporate the criterion of a network recommendation in their evaluations due to its subjectivity. Network recommendations were described as subjective and informal, while still recognizing they are influencing perceptions of applicants when observed for one applicant but not for another. Interestingly, while interviewees further indicated a network recommendation may be difficult to get for women, they valued it especially in women.

The findings indicate that gender stereotypes play a role in many different forms and can be part of heuristics and can also influence judgments based on objectively observable signals. Therefore, to move towards a comprehensive understanding of assessments in appointment committees, influences on different levels, in different domains, and in different stages of the recruitment process need to be considered. Clearly defined and objectively assessable criteria can be highly valuable, particularly in earlier stages of recruitment, while in later discussions additional heuristics and in turn gendered arguments may come to play.

Practical implications

Although recruitment for STEM professorships generally promotes clearly defined and objectively amenable criteria for assessment and selection, subjective discussions of applicants still make a large part of the process. Adding more structure to those discussions can help to objectify the processes. For

instance, appointment committees should discuss and agree on specific criteria *before* sharing information about applicants or starting to discuss their suitability (see, e.g., Heilman, 2012). Not all committee members may have the same information about the position and prior considerations at job advertising (see also van den Brink and Benschop, 2012). STEM professors play a crucial role in creating and promoting a picture of the diverse and actual requirements of the jobs (Rehbock et al., 2021) rather than collapsing into a stereotypical assessment pattern of how they think STEM professors typically are or are expected to be like when evaluating *others'* suitability (see, e.g., Male et al., 2009). With clearly defined criteria and requirements, appointment committees can define the signals to look for in applicants, and the questions asked to obtain information about certain applicant qualities that fulfill the desired profile. For instance, committee members can reflect on whether appearing highly self-confident when presenting one's achievements is a requirement (e.g., to master demands such as heading executive education), or simply corresponds more with the stereotypical image whereas abilities to be self-critical and self-reflective are the more valuable qualities for scientists.

In addition, training committee members is crucial for them to not only be aware of gendered arguments but also learn ways to recognize and challenge those arguments (see, e.g., Horvath, 2018). For example, the committee chair can assign a trained committee member the role of a devil's advocate challenging assumptions made about applicants that are not yet verified or lack reliable information cues for verification.

STEM professors are not only part of necessary change as committee members; they can further be role models promoting a diverse image of STEM professors and different possible academic life tracks. This includes normalizing parental leaves, as well as efforts towards a more inclusive work climate in STEM fields such that there is no question that women may feel uncomfortable or have problems integrating. Universities further need to increase their efforts of demonstrating how academia is a good working environment to balance work and family for professors of all genders, actively considering the needs of care takers and providing enough help and structures that align with care taking responsibilities (see, e.g., Greider et al., 2019). In general, there is a need to normalize that women, same as men, are pursuing science (Müller, 2021). The paradox of women's exceptional status shows that, as long as femininity is perceived as deviance, regulations need to be set and closely monitored to ensure that women are considered in recruitment, while potentially creating a perceived female advantage.

Finally, we can derive recommendations for female applicants for STEM professorships. They cannot directly influence the discussions in appointment committees. However, knowing what aspects are potentially problematized in female more than in male applicants, female applicants can provide information cues as counter signals of questioning their ability, general traits, and commitment. For instance, they can signal they have a realistic job preview and clearly state the abilities and past achievements helping them to meet the requirements; they can describe how they are part of the STEM community and will integrate into the faculty (e.g., describing planned cooperation and committee work); and they can emphasize their commitment to research and teaching. Indeed, prior research showed that a "maybe baby" penalty female applicants are facing is reduced when female applicants emphasize their commitment to work (Peterson Gloor et al., 2021).

Furthermore, our finding that particularly female applicants may profit from a network recommendation highlights that efforts of women to get inroads into networks and work with well-known senior scientists likely pay off. Problematic is that networks in (STEM) academia are often made for and by men and women can only influence to a limited extent whether they are perceived as "being part of it" (van den Brink and Benschop, 2014).

Limitations and future research

In the current research, we implemented a mixed methods approach to capture both gendered arguments and gendered success patterns. Our approach was particularly qualified to model applicant assessments in a qualitative research approach, while additionally gathering quantitative ratings based on objectively observable applicant attributes. While this approach helped us to understand the full picture of influences of heuristics, stereotyping, and signals, it also has some limitations.

In our exploratory approach we did not test specific hypotheses. However, based on our findings, propositions to be tested in future field survey and experimental research can be derived. For instance, more closely investigating the paradox of women's exceptional status in STEM careers is of high practical relevance, including the questions of whether a perceived exceptional status is more or less pronounced, or has a different connotation, depending on, e.g., male-typed hobbies of female applicants, the perception of maternity, or prior failures of women in similar positions. Moreover, questioning behavior towards male vs. female applicants needs further investigation in a quantitative study (similar to Kanze et al., 2018).

Furthermore, social desirability may have played a role in our interviews. The interviewee's and interviewer's identity were disclosed. Thus, to some extent, our interviewees may have been inclined to answer in a socially acceptable way. Yet, we declared anonymized handling of the gathered data and statements used to illustrate our points will not allow conclusions about individual interview partners. The overall impression further was that most of the interviewed professors talked quite openly about their experiences in appointment committees (while some considered themselves as having a greater gender equality mindset than other appointment

committee members typically have). Additionally, for their quantitative ratings, the interviewees filled out a survey that was processed anonymously.

The assessment scenario construed for professors' ratings was a simplification of reality as a limitation of experimental designs. Using a conjoint experiment, we could look at different applicant attributes simultaneously. However, in practice, applicant attributes and their levels are more complicated than how they were modeled in the conjoint experiment, and applicants are less comparable in reality. Nevertheless, the conjoint experiment can show how objectifying the process, i.e., evaluating applicants on comparable criteria and signals, can foster gender equality. Furthermore, although the interviewees did not make actual decisions on applicants, they considered the applicant attributes to reflect relevant and realistic criteria. Furthermore, due to our think aloud approach, they could add criteria they think are important or share other additional thoughts or comments on applicant evaluations.

Last, the generalizability of our findings to other contexts than STEM professorships may be limited. Although we can draw parallels from (perceptions of) professors to other leaders (Braun et al., 2013; Dutz et al., 2022; Rehbock et al., 2022), some criteria for the assessment and selection of professors do not matter in industry contexts (e.g., publications).

Conclusion

Recruitment contexts such as recruitment for STEM professorships promote selection criteria clearly defined and objectively assessed; illuminating the subjective interpretation of seemingly objective criteria, and gendered arguments in applicant assessments in theses contexts, our findings corroborate that they are not as objective as they seem. Still, our findings suggest that relying on specific signals that are at least objectively observable can objectify applicant assessments and thus foster gender equality. Importantly however, objectively observable signals need to be carefully defined and still cannot eliminate gender bias completely.

Data availability statement

The datasets generated for this study are available on request to the corresponding author.

Ethics statement

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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REVIEW
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An Evolutionary Explanation for the Female Leadership Paradox

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Social influence is distributed unequally between males and females in many mammalian societies. In human societies, gender inequality is particularly evident in access to leadership positions. Understanding why women historically and cross-culturally have tended to be under-represented as leaders within human groups and organizations represents a paradox because we lack evidence that women leaders consistently perform worse than men. We also know that women exercise overt influence in collective group-decisions within small-scale human societies, and that female leadership is pervasive in particular contexts across non-human mammalian societies. Here, we offer a transdisciplinary perspective on this female leadership paradox. Synthesis of social science and biological literatures suggests that females and males, on average, differ in why and how they compete for access to political leadership in mixed-gender groups. These differences are influenced by sexual selection and are moderated by socioecological variation across development and, particularly in human societies, by culturally transmitted norms and institutions. The interplay of these forces contributes to the emergence of female leaders within and across species. Furthermore, females may regularly exercise influence on group decisions in less conspicuous ways and different domains than males, and these underappreciated forms of leadership require more study. We offer a comprehensive framework for studying inequality between females and males in access to leadership positions, and we discuss the implications of this approach for understanding the female leadership paradox and for redressing gender inequality in leadership in humans.

Keywords: leadership, gender, hierarchy, evolution, ecology, mammals, cooperation, collective decision-making

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INTRODUCTION

Across all contemporary industrialized societies, women remain underrepresented in boardrooms and governments, holding fewer than 6% of CEO positions at S&P 500 companies (Thomas, 2018) and fewer than 5% of national political leadership positions in the world. While this gender gap has been narrowing (Geiger and Kent, 2017; Bartleby, 2019), the challenges women face in climbing the corporate and political ladder remain substantial (Ryan and Haslam, 2005; Marshall et al., 2017; Kirsch, 2018). A male bias in top positions of leadership is a near cross-cultural universal: in a

large sample of historical and contemporary non-industrial societies, formal political leadership positions were exclusive to men in approximately 88%. Among the 10% of societies in which women did occupy leadership positions they were either less numerous or less powerful than their male counterparts (Whyte, 1978). Why have women been less likely to make it to the top ranks in politics, business, science, and religion, whether cross-culturally or historically? This is a paradox given that there is no consistent evidence that women make worse leaders in terms of their traits (Eagly et al., 2003; Post, 2015; Yang et al., 2019), women exercise considerable political influence in many small-scale, more egalitarian human societies (Leacock, 1978; Wiessner, 2005; von Rueden et al., 2018), and female leadership is pervasive, particularly in some contexts, across non-human mammalian societies, even in species where males tend to dominate females in dyadic competition (Smith et al., 2020). In our contribution to this inter-disciplinary research topic, we explore this female leadership paradox from multiple disciplinary perspectives. Furthermore, we unite these perspectives into a framework that helps explain variation in female and male leadership across and within species, including humans.

In the human social sciences, scholars have in general attempted to explain the gender gap in leadership principally in terms of proximate factors such as gender stereotypes, glass ceilings, and institutional sexism (Koenig et al., 2011; Matsa and Miller, 2011; Hideg and Shen, 2019). Other scholars have invoked evolutionary theory to suggest that evolved motivations contribute to but do not fully determine nor justify observed leadership patterns (Low, 1992; Smuts, 1995; von Rueden et al., 2018). An implication of such evolutionary approaches is that once we identify these evolved motivations, then we, as a cultural species, can make more informed decisions about how to remove obstacles for women leaders (Smith et al., 2020). Furthermore, evolutionary approaches that make comparisons among species suggest that the study of leadership in the social sciences is often narrowly defined (e.g., in terms of who is in charge), analyzed in specific domains (e.g., military, business, politics), restricted to narrow goals (e.g., conflict management), and restricted to a subset of societies [e.g., Western, educated, industrialized, rich and democratic (WEIRD)] (van Vugt and Ahuja, 2011). If we broaden the scope of leadership to not just include the more conspicuous forms of leadership (e.g., the CEO, the president, the priest), then we see much more evidence of females exercising influence in collective decision-making.

In general, we will argue that evolutionary theory, which predicts sex-specific yet environmentally contingent behavioral strategies (Clutton-Brock and Huchard, 2013b), can be complementary to traditional social science explanations of gender differences in leadership patterns. We define leaders as those individuals who have disproportionate influence, including decision-making power, on collective behavior (Pyritz et al., 2011b; Smith et al., 2016). It is important to emphasize that leadership should not be conflated with dominance (see next section), with the latter defined instead as the power to win fights or coerce others to gain priority of access in a resource hierarchy (deWaal, 1986; Hand, 1986; Van Vugt and Smith, 2019). Thus, whereas dominance refers to coercive influence within the group's resource hierarchy, leadership refers to influence within the group's decision-making processes and need not be coercive. Leadership can involve overt or more subtle forms of influence (e.g., direct intervention vs. example-setting), vary across individuals according to the context, and be distributed across group members or be concentrated in a single individual within a context (Glowacki and von Rueden, 2015; Smith et al., 2016; Smith and van Vugt, 2020). For example, in some non-human societies, leaders may actively break-up fights (e.g., prosocial policing by rhesus macaques; Beisner and McCowan, 2013) whereas in others leaders simply recruit followers by moving first (e.g., group travel to water by zebra; Fischhoff et al., 2007) or targeting a prey animal (e.g., group hunting by lions; Packer et al., 2001).

We use the term gender when referring to humans because of the influence of cultural norms on differences in behavior across men and women, and we use the term sex when referring more broadly to mammals. In fact, because gender is defined as the perceived sex (Money et al., 1955) or some other perceived identity related to sex, and we have no way of knowing whether and how animals may perceive themselves, the application of the gender concept in animals is inappropriate (Goymann and Brumm, 2018). Our focus on sex and gender differences is not meant to obscure the comparatively much larger variation for most behaviors observed within sexes and genders (Archer, 2019; Hyde et al., 2019), nor is it meant to argue that sex and gender are necessarily binary. Rather, we focus on behavior that does often vary moderately or considerably according to sex and gender categories. Some of the largest sex and gender differences are evident in particular cooperative and competitive behaviors (Zell et al., 2015; Archer, 2019), which can be compared across species, may be tied in part to processes of sexual selection, and are frequent targets of cultural norms.

We focus our synthesis on two potential factors contributing to observed gender differences in access to leadership in humans: (i) women and men tend to differ in how they cooperate and compete in the pursuit of leadership, and (ii) the perception by followers that women lack the "appropriate" leadership qualities. As we will argue, men and women, on average, often differ in what motivates the pursuit of leadership positions, and in strategies for acquiring leadership (e.g., direct vs. indirect competition, risk tolerance, differences in building and leveraging social connections). Moreover, studies at least in WEIRD societies show that potential followers often show implicit and explicit biases against overt forms of leadership by women (Rudman and Kilianski, 2000; Ridgeway, 2001; Simon and Hoyt, 2008; van Vugt and Spisak, 2008; Hoyt and Burnette, 2013). For instance, women may frequently be perceived as lacking in "agentic" traits (e.g., assertiveness, dominance) deemed necessary for good leadership; moreover, if women show agency they may receive negative reactions for violating gender stereotypes (Rudman and Phelan, 2008).

We construct a framework to explain these related phenomena, which integrates studies regarding the (a) evolutionary history (e.g., patterning across mammalian species), (b) human cultural history, (c) ecological function (e.g., fitness consequences), and (d) developmental origins

of sex and gender differences in leadership. We divide our review into sections according to these levels of explanation. In addition, we emphasize throughout our review the role of socioecological variation across and within species as a source of sex and gender differences in competition for leadership, in the fitness consequences of such differences, and in their development. In humans, such socioecological variation includes culturally transmitted institutions and norms, for example those regarding gender divisions of labor and wealth inheritance. These institutions and norms influence and are influenced by gender differences in competition, as well as beliefs regarding "appropriate" leadership qualities and even what defines leadership. Our framework distinguishes direct effects of sexual selection on men and women's motivations and strategies, from indirect effects of sexually selected traits in terms of their contribution to (but neither determination nor justification of) cultural transmission of institutions and norms delineating rights and expectations by gender (Eagly and Karau, 2002). By identifying broad patterns across human and non-human societies as well as convergences between evolutionary and traditional social science theories, our framework provides a comprehensive and powerful explanation of sex and gender disparities in leadership. Furthermore, as we discuss at the end of our review, such a more comprehensive framework has unique implications for redressing gender inequality in access to leadership positions for humans.

EVOLUTIONARY ORIGINS OF SEX DIFFERENCES IN LEADERSHIP

A comparative perspective offers insights into what is universal and what is variable in terms of leader emergence according to sex, as well as the ancestral states and evolutionary transitions that account for what is universal and what is variable (Smith et al., 2016, 2020; Kappeler, 2017; Brosnan, 2018; Kappeler et al., 2019). Whereas power (French and Raven, 1959), dominance (Bass and Bass, 2009) and status (Cheng et al., 2010) are often used interchangeably to describe human behavior, this can be confusing from a comparative perspective (Van Vugt and Smith, 2019). Across species, individuals that influence collective decisions can be also high-ranking in the dominance hierarchy, as in the handful of mammals for which females are socially dominant to males (Smith et al., 2020). In mammals, female dominance is rare, but when it does occur, it is typically mediated by a larger body size and strength in females relative to males (Kappeler, 1993; Lewis, 2018; Smith and van Vugt, 2020). For biologists, dominance describes an individual's ability to gain priority of access to resources by winning dyadic fights with another individual (deWaal, 1986; Drews, 1993). In some species, individuals can also enhance access to resources via coalitional support (Harcourt and de Waal, 1992; Smith et al., 2010; Bissonnette et al., 2015). Importantly, however, leaders are neither necessarily always dominants nor *vice versa* (Fichtel et al., 2011; Van Vugt and Smith, 2019; Smith and van Vugt, 2020). The same is true of the relationship between leadership and sources of social status distinct from dominance, such as leverage (Lewis, 2002) or prestige (Henrich and Gil-White, 2001; Cheng et al., 2010). Thus, leadership, dominance, and other forms of social status require conceptual separation in studies of human and/or mammalian behavior (Henrich and Gil-White, 2001; Conradt and List, 2009).

Focusing on leadership within a broad cross-species perspective yields at least four novel insights. First, leadership is heterogeneous: leadership emerges in multiple contexts, including group movement, subsistence/foraging, within-group conflict resolution, and between-group interactions (Smith et al., 2016). In non-human mammals, the emergence of leaders in these contexts is typically more achievement-based (e.g., based on a leader's actions, age or strength) compared to human societies (Smith et al., 2016) where inheritance of wealth, formal titles, or social identities like race and gender often determine leadership (Garfield et al., 2019). However, inherited rank based on kinship contributes to leader emergence in those non-human mammals for which leaders may also tend to be of high dominance rank (Harcourt and de Waal, 1992; Smith et al., 2010), and some human societies, particularly most observed hunter-gatherers, lack leadership inheritance (Garfield et al., 2019). Leadership also varies in its distribution across group members. In non-human societies, leadership is often distributed among multiple individuals (Strandburg-Peshkin et al., 2016, 2018). That is, collective behavior is initiated and coordinated by several individuals even in groups with either steep or flat dominance hierarchies, such as those of baboons and some lemurs, respectively (Trillmich et al., 2004; King et al., 2008; Pyritz et al., 2011a). A fundamental difference between leadership in human and non-human societies is that, in humans, a centralized leader (or leaders) typically assign(s) tasks to different individuals to achieve a collective goal. In this case, followers share common intentions to produce an explicitly managed good. In contrast, non-human group movements and other collective behaviors emerge from individual behavioral decisions, often without explicit coordination by leaders (Couzin and Krause, 2003; Willems et al., 2015; Koch et al., 2016a,b; Willems, 2016).

Second, sex-biased leadership across mammalian societies is infrequent. Year-round permanent association of males and females occurs in only about a third of all mammalian species; non-human primates being a notable exception with about 70% of species forming bisexual groups (Van Schaik and Kappeler, 1997). Moreover, males and females in permanently bisexual groups tend to establish minimally overlapping dominance hierarchies and/or interact primarily with members of the same sex, as seen for example across all major primate radiations (Fedigan and Baxter, 1984; de Waal and Luttrell, 1985; Kappeler, 1990a,b; Foerster et al., 2016), representing a potential constraint on the formation of cross-sex leader–follower relationships. Against this background, the uniqueness of gender-integrated decision-making hierarchies within the groups and organizations of human societies requires explicit acknowledgment in future studies of gender biases in leadership. Competition for leadership in mixed-gender groups can exacerbate gender inequality in access to overt leadership positions, because of gender stereotypes

that portray women as less leader-like than men (Hegstrom and Griffith, 1992; Chen and Houser, 2019).

Third, sex-typical leadership roles in mammalian societies can vary by relevant socioecological context (Smith et al., 2020). In general, sex-specific fitness incentives contribute to patterns of leadership with a tendency for females to take the lead in contexts that affect the group's safety and ability to locate resources (see **Figure 1**), and a tendency for males to contribute more in contexts related to securing reproductive opportunities such as in between-group conflicts. However, there is much variation within and across species that complicates these sex-specific tendencies, as we discuss in the section on ecological functions of sex differences in leadership.

Fourth, sex differences in life history decisions (e.g., patterns of dispersal and reproduction) for male and female mammals can also have downstream consequences for social behaviors related to leadership. Since females in most mammalian societies are philopatric, they form kin-based coalitions more than males, who typically disperse from their natal group (Wrangham, 1980; Kappeler and Van Schaik, 2002; Smith, 2014; Smith et al., 2017). In chimpanzees and bonobos, however, these sex roles are reversed, theoretically advantaging male (vs. female) coalition building through kin-selected benefits. Female bonobos nonetheless build coalitions with non-kin, providing an important role in internal peacekeeping and other aspects of group decision-making (Surbeck et al., 2011; Tokuyama and Furuichi, 2016). Female philopatry also provides female elders greater opportunities to use specialized ecological knowledge that benefits followers, particularly in species with exceptional longevity such as elephants or orcas (McComb et al., 2001; Brent et al., 2015). In humans, the evolution of unique life history traits created new opportunities and constraints for gender-specific leadership. Decreased inter-birth intervals and longer juvenile periods in concert with biparental care and a skill-intensive foraging niche promoted gender division of labor within extended families (Kaplan et al., 2009; Alger et al., 2020). The relative contribution of men and women to the diet, as well as gender

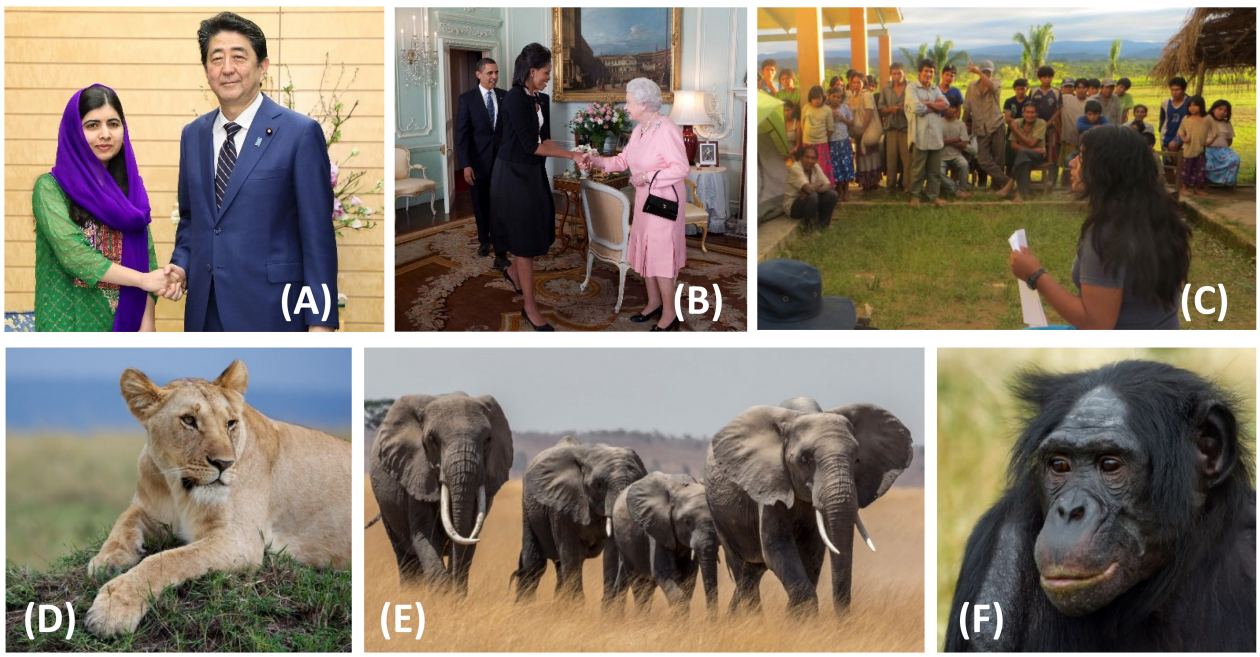

FIGURE 1 | Female leadership across mammalian societies. Women influence collective decisions in a variety of ways, as illustrated by **(A)** Malala Yousafzai (Pakistani activist for female education) shaking hands with Shinzô Abe (former Prime Minister of Japan), **(B)** Michelle Obama (first African American first lady of the United States and advocate for equity and inclusion) and Her Majesty, Elizabeth, II (Queen of the United Kingdom, a position inherited as the first born to King George VI and Queen Elizabeth), and **(C)** Agustina Bani of the Tsimané (leading discussion aimed to improve health outcomes in her Bolivian community). Among non-human mammals, strong female leadership is particularly well understood for eight species (Smith et al., 2020). Three of these species (not shown here) live in female-dominated societies: spotted hyenas (Boydston et al., 2001; Smith et al., 2010, 2015), ring-tailed lemurs (Nakamichi and Koyama, 1997; Sauther et al., 1999) and black-and-white ruffed lemurs (Morland, 1991; Overdorff et al., 2005). In all three species, females are at least as large or larger and stronger than males, suggesting a role for body size and fighting ability in promoting access to overt forms of female leadership. However, other societies promote female access to leadership through perhaps less overt forms, such as female cooperation; for example, **(D)** African lionesses lead in cooperative hunting and protection of offspring (Packer et al., 2001) and **(F)** female bonobos join forces to resolve tension and within-group conflict (deWaal, 1995; Furuichi, 2011; Tokuyama and Furuichi, 2016). Finally, females with specialized knowledge may emerge as leaders, as occurs in **(E)** African elephants for which the female matriarch serves as a repository of knowledge, leading group travel (McComb et al., 2001; Wittemyer and Getz, 2007) as well as in bonobos (Tokuyama and Furuichi, 2017) and killer whales (also not shown here; Foster et al., 2012; Brent et al., 2015). Just as in human societies, multiple pathways to female leadership exist in the natural world and these examples help to uncover the diverse and often underappreciated ways that females exert influence on collective behavior. (Photos by S. Richards, R. Bergstrom, Phôs Graphé, P. Souza, and P. Hooper with permission or part of the public domain).

specialization in particular forms of food production, vary across observed hunter-gatherers according to habitat seasonality and other ecological factors (Marlowe, 2007), but in general women tend to engage in significantly more direct childcare (Kramer, 2010). To the extent aspects of gendered division of labor afford men more opportunity for broad-based social networking and wealth accrual within and across communities, it can make male-biased leadership beyond the household more likely (von Rueden et al., 2018), as we explain in subsequent sections.

HISTORY OF GENDER INEQUALITY IN HUMAN SOCIETIES

Although the comparative perspective offers insights into sex differences in leadership access and preferences across the mammalian lineage, examination of the unparalleled intraspecific variation in human social systems is also crucial for explaining the origin and diversity of human leadership (**Table 1**). An appreciation of human social and cultural diversity in space and time reveals that many modern and historical forms and functions of human leadership are relatively recent features of human sociality. Humans spent more than 95% of their existence as hunter-gatherers (Marlowe, 2005). While the modal pattern for modern hunter-gatherers is residence in groups of ∼30 individuals (Bird et al., 2019), social networks might expand to hundreds of individuals over a person's lifetime due to fluidity in residence, trading partners, and kinship (Layton et al., 2012; Bird et al., 2019). A minority of hunter-gatherers who occupied highly productive coastal or riparian environments were led by chiefs with some degree of coercive authority, and the frequency of such "complex" hunter-gatherer societies may have been significantly higher in the Pleistocene prior to expansion of agricultural practices in the Holocene (Singh and Glowacki, 2021). Nevertheless, the majority of modern hunter-gatherers, if not hunter-gatherers in general, were relatively egalitarian with high degrees of autonomy for individuals (Kelly, 2013).

Many factors contribute to human egalitarianism, including pair bonding between men and women that reduces mating competition (Gavrilets, 2012), the ability for individuals or families to "vote with their feet" in the event of conflict via flexible residence patterns that are neither strictly patrilocal or matrilocal (Marlowe, 2005), an ability to form coalitions against would-be dominants (Boehm, 1999), reliance upon difficult to acquire food (which motivates extensive cooperation within and among families; Kaplan et al., 2009; Smith et al., 2012), and prestige-driven cooperation dynamics in which status depends on cooperation with lower status group members (von Rueden et al., 2019). Leadership exists in even the most egalitarian societies, whereby certain individuals wield more influence than others in the course of group decision-making. However, group decision-making remains largely consensus-based (von Rueden et al., 2014; Garfield et al., 2019). Women regularly influence group decisions in hunter-gatherer and other small-scale subsistence societies (Leacock, 1978), particularly in domains such as marriage and residential decision-making (Dyble et al., 2015) and informal dispute resolution (Radcliffe-Brown, 1948; Bowser and Patton, 2010). Women in small-scale societies are also often noted more than men for their public criticism of non-normative behavior (e.g., Wiessner, 2005; Lewis, 2014). The latter can be a means for women to use men to advance their political goals, by turning private knowledge into common knowledge that forces the community or kin group to act. In some small-scale societies, women assume political leadership within their own religious and political organizations, such as in many Aboriginal societies (Dudgeon and Bray, 2019). However, even in some of the most egalitarian hunter-gatherer societies, women have been described as on average less politically influential relative to men, or as less frequent organizers of meetings to coordinate camp-wide activities (Radcliffe-Brown, 1948; Lee, 1980; Collier and Rosaldo, 1981; Lewis, 2014).

How gender affects leader emergence, even in the most egalitarian human societies, is likely in part due to sexually selected differences in competition and cooperation (see next section), as well as their contribution to culturally transmitted and enforced gendered divisions of labor. The latter is often based around the pair bond: women are typically expected to perform more labor within the house and men more labor outside of it (von Rueden et al., 2018). Though variable cross-culturally in its form and magnitude, gender division of labor is relatively ubiquitous across human societies. Anthropologists have long tied gender inequality in political influence in both small and large-scale societies to gendered divisions of labor, which may constrain women's networking within and between communities and accord men more opportunity to amass and control wealth (Leacock, 1978; Coontz and Henderson, 1986).

The incidence of coercive leadership – recently referred to as dominance style leadership (Cheng et al., 2013; Maner, 2017; Van Vugt and Smith, 2019) – ratcheted up with the Neolithic revolution, when peoples' main subsistence strategy shifted from nomadic foraging to sedentary agriculture (**Table 1**). Dominance style leaders exercise their influence on group decisions by inflicting (or threatening to inflict) costs on non-followers whereas prestige style leaders instead influence group decisions by conferring (or promising to confer) benefits on followers (Van Vugt and Smith, 2019). Agriculture increased the incidence of dominance style leadership due to effects of agricultural surplus on demographic change and wealth inequality. Agricultural surpluses fueled population growth through increased reproductive rates, creating demand for centralized leadership with coercive powers to quell conflict and coordinate large-scale cooperation such as in warfare or food production (Hooper et al., 2010; von Rueden, 2020). Once granted coercive powers, leaders could then expand them to their advantage (Powers and Lehmann, 2014). Furthermore, kin-based lineages that could monopolize the most productive land and generate more surplus production asserted exclusive rights to leadership, by controlling the labor of the less privileged (Mattison et al., 2016). Of course, dominance-style leadership in humans cannot rest on coercion

TABLE 1 | Human social diversity in space and time contributing to leadership.

Social organization	Size	Subsistence	Mating system	Inheritance	Inequality	Political leadership	
Shifting co-residence of community members within residential bands	10^2–10^3	Nomadic foraging or horticulture	Monogamy w/ minimal polygyny	Mostly bilateral	Egalitarian	Distributed leadership or informal headmen	
Tribal societies, subdivided into clans, lineages, moieties, and other symbolically marked groups	10^3–10^5	Sedentary foraging, horticulture, pastoralism, or agriculture	Minimal to significant polygyny	Mostly unilateral (patriliny or matriliny)	Minimal to significant stratification by wealth	Big men or chiefs	
States or Empire	10^4–10^7	Agriculture and/or industry	Significant polygyny or socially imposed monogamy	Patriliny or bilateral	Significant stratification by wealth	King/Queens 	Elected leaders 

A prevailing view is that for hundreds of thousands of years, humans were organized largely in small, residential bands with flexible, fluctuating membership and with relatively egalitarian politics (Kaplan et al., 2009; Layton et al., 2012; Diamond, 2013; Van Schaik, 2016). Recent evidence suggests sedentary foragers with institutionalized hierarchies may have been more common in the past (Singh and Glowacki, 2021), nevertheless the onset of agriculture was key to the widespread erosion of egalitarianism and the emergence and spread of formal, often coercive leadership (van Vugt et al., 2008; Kaplan et al., 2009). The social power of women in non-industrial societies in part reflected the prevailing inheritance systems, with bilateral descent/matriliny offering more opportunities for female social influence (Low, 2005). Variation in leader archetypes across different forms of human social organization constitutes at least an order of magnitude more of intraspecific variation than any non-human animal society studied so far. Several examples of this extraordinary intraspecific variation are represented (from top to bottom) by images of a male hunter from the Hadza foragers near Lake Eyasi in Tanzania, a Huli wigman from the Southern Highlands of Papua New Guinea, Mswati III who is currently the King of Eswatini (formerly Swaziland) and head of the Swazi royal family, and Kamala Devi Harris who is currently serving as the highest-ranking female official in United States history as Vice President of the United States. Photos were taken by A. Peach, A.-J. Gros from The Yorck Project, A. Lucidon, and L. Jackson are public domain.

alone; autocrats must reward a large-enough coalition of powerful individuals to stave off revolution by the masses (Pandit et al., 2020).

Increasing inequality in political leadership brought with it increasing gender inequality. Monopolizable wealth likely increased men's motivation and opportunity to form large alliances with other men to control, defend, and compete for resources, enabling greater control over the reproductive decision-making of women (Smuts, 1995). Men's larger-scale alliance building was reinforced by increased threats and opportunities of inter-group conflict and warfare (Hayden et al., 1986; Rodseth, 2012) and by more restrictive gendered divisions of labor. Gender division of labor varies across societies according to local subsistence practices and economic opportunities (Starkweather et al., 2020). For example, the introduction of the plow made agricultural labor more strength-intensive and less compatible with childcare, thereby decreasing women's labor value outside of the home, decreasing women's bargaining power, and decreasing women's access to leadership (Alesina et al., 2011). Changing division of labor brought about new gender norms of what behavior is expected of men and women.

A minority of agricultural societies, particularly those with small to moderate amounts of material wealth, were matrilineal (i.e., descent traced from mother to daughter rather than father to son). Women may have most frequently acquired formal political leadership in those pre-industrial societies with matrilineal descent (Low, 1992). In the Iroquois confederation, for example, senior Iroquois women appointed and removed male chiefs and could veto their decisions, and Iroquois women arranged marriages and were as likely as men to be religious leaders (Brown, 1970). Men in matrilineal societies wield authority in terms of their relationship to the matriline, so mother's brothers nominally have the most authority in group decisions. However, the nominal authority of men in matrilineal societies may often contrast with real authority wielded by women, particularly at the household level (Mattison et al., 2019).

In contrast, patriliny exacerbated patriarchy, by increasing opportunities for large-scale male coalition building, distancing women from their kin, and entrenching male control over group decisions (Smuts, 1995; Wood and Eagly, 2002). Patriliny was more likely to emerge as societies became wealthier, in part because of the relationship between polygyny and wealth and thus the increased value to men of investing in their sons (Mattison et al., 2019). Political inequality ratcheted up further in early states, where a small elite spearheaded by a central ruler claimed a monopoly of force. While states have been more or less patriarchal, familial ties could promote a niche for women leaders, such as Queen Victoria (Schönpflug, 2010), to inherit powerful positions of leadership. Only recently have states tended to become less coercive, with multi-tiered leadership structures subject to approval of followers (Trouillot, 2001; van Vugt et al., 2008; Boehm, 2012; Diamond, 2013; **Table 1**).

ECOLOGICAL FUNCTIONS OF SEX DIFFERENCES IN LEADERSHIP

Sexual Selection and Sex-Specific Leadership

Fitness costs and benefits associated with leadership decisions in animals are distinct from, but sometimes related to, those associated with dominance. For example, leaders within a group may influence group decisions to travel toward a food resource or to cooperatively capture prey, whereas dominance status determines an individual's priority of access to that food resource once it is located or acquired by a group. In the context of intergroup conflicts over territory boundaries, leaders influence when to initiate a fight and for how long (e.g., Boydston et al., 2001), whereas dominants determine who gains access to resources contained within a shared territory (e.g., Frank, 1986; Smith et al., 2008).

Because leadership is associated with individual costs and benefits, it is meaningful to ask whether these cost-benefit ratios vary systematically between the sexes across mammals. Sexual selection is expected to favor (1) sex differences in the pursuit of leadership in contexts for which the net benefits of leadership differ by sex. In addition, sexual selection can favor (2) sex differences in strategies of cooperation and competition, which can affect sex differences in the opportunity and motivation to lead in any context. A general prediction consistent with interpretations of sexual selection theory is that female mammals may be less motivated than males to pursue leadership that enhances mating opportunities at a cost to parental investment. According to the Bateman-Trivers paradigm (Bateman, 1948; Trivers, 1972), for example, males in many, but not all, species have a higher potential reproductive rate than females, primarily due to sex differences in parental investment (Kokko and Jennions, 2008; Clutton-Brock, 2017). Put differently, the number of reproductively available males tends to be greater than the number of reproductively available females, i.e., the operational sex ratio (OSR) is male-biased (Emlen and Oring, 1977). As a result, sexual selection related to direct competition for mates is expected to be stronger for males, whereas females are selected to maintain or increase total parental investment, such as via gestation and lactation in mammals (Trivers, 1972; Clutton-Brock and Huchard, 2013a; Fromhage and Jennions, 2016). When females invest more in parental investment, female fitness is generally more limited by access to resources than is male fitness, whereas male fitness is generally more limited by access to fertile females. We will show below that these sex differences in resource limitation can also influence sex differences in leadership to in turn influence group decision-making.

While a strong consensus remains among biologists that female mammals in general and female primates in particular invest more than males in the energetically costly post-mating activities of gestation and lactation (Emlen and Oring, 1977; Kappeler and Van Schaik, 2002), the Bateman-Trivers paradigm has been heavily critiqued (Tang-Martínez, 2016); recent data (Gowaty et al., 2012, 2013) reveal that Bateman's (1948) measures of fitness variance were flawed and that the cost per gamete assumption of Trivers (1972) is problematic (Kokko and Jennions, 2008). Sex differences in post-mating investment can favor greater male than female intra-sexual competition for mates, but this may attenuate or, less frequently, reverse in response to high variation in male mate quality, male parental investment, or mating market factors that create female-biased sex ratios (Ralls, 1976; Kokko and Jennions, 2008; Brown et al., 2009; Rosvall, 2011). Furthermore, the effect of OSR on sexual selection can weaken as the OSR becomes increasingly biased, such as when an increasing number of rivals makes aggressive competition especially costly (Weir et al., 2011). And the effect of OSR on sexual selection can differ for different traits. Across animal species, higher OSR associates with increased mate guarding and aggression toward competitors but decreased courtship behavior (Weir et al., 2011).

Despite the aforementioned limitations, recent analytical models still confirm key insights of Bateman-Trivers (e.g., Fromhage and Jennions, 2016), and the general pattern of greater male investment in mate competition and greater female investment in parental investment continues to receive general empirical support across the animal kingdom (Janicke et al., 2016). Moreover, theoretical critiques of the Bateman-Trivers paradigm have helped explain the tremendous variation within and across species in sex-specific mate competition and parental investment (Clutton-Brock and Huchard, 2013b; Henshaw et al., 2019). Taken together, these differences in post-mating investment strategies can influence decisions regarding how, when, and why females versus males compete for opportunities to lead in collective decisions.

In terms of leadership, females can better meet their own and their offspring's energetic needs by leading (vs. following) members of their group to particular resources and by deciding how long to use them, as occurs in plains zebra (Fischhoff et al., 2007), bonobos (Tokuyama and Furuichi, 2017), muskoxen (Ihl and Bowyer, 2011), and lemurs (Pyritz et al., 2011a). Post-menopausal killer whales increase their own fitness by leading their sons to scarce resources (Brent et al., 2015). Males may also lead group foraging decisions, but perhaps less frequently to benefit offspring. Experiments with chacma baboons found that dominant males were most likely to lead groups to new food patches because they could monopolize the resources once obtained, and follower behavior was mediated by social ties to the dominant male (King et al., 2008). In muskoxen, although followers are generally most likely to follow adult females, males actively herd and block females to coordinate group movements during the breeding season (Ihl and Bowyer, 2011).

In the context of intergroup conflicts, studies of chimpanzees (Williams et al., 2004) and white-faced capuchins (Perry, 1996) suggest that border patrols and participation in intergroup conflicts are instead almost exclusively male activities; male participation increases access to mating opportunities (Wilson and Wrangham, 2003). In the context of intragroup conflict, observations of both chimpanzees and bonobos also suggest females tend to recruit coalition partners primarily to defend kin and friends against male aggression, whereas males tend to build coalitions primarily to compete for high rank and the mating opportunity it affords (Newton-Fisher, 2006;

Tokuyama and Furuichi, 2016). However, a recent metanalysis of relevant primate studies revealed only weak support for the effect of sex on the frequency of aggression displayed toward outgroup individuals during intergroup encounters (Majolo et al., 2020). Moreover, the meta-analysis found significant variation in female participation in intergroup aggression across and within species (Majolo et al., 2020). In rare cases for which female mammals are the dominant sex, females also commonly lead intergroup conflicts and can be just as aggressive as males, as is seen in Verreaux's sifakas (Koch et al., 2016a) or ring-tailed lemurs (Nunn and Deaner, 2004). Moreover, in spotted hyenas, dominant females also influence group decisions by leading in intergroup conflicts significantly more often than males (Boydston et al., 2001). In vervet monkeys, females lead by initiating intergroup conflicts (to usurp food from other groups) and harass lower-ranking males to participate (Arseneau-Robar et al., 2017); females of this species, however, can be punished by dominant males for trying to escalate costly inter-group conflicts (Arseneau-Robar et al., 2018).

The costs of leading in different contexts also pattern sex differences in leadership. Costs of leadership in social mammals include enhanced predation risk (e.g., individuals that move first; Bumann et al., 1997) and synchronization costs (e.g., opportunity costs associated with building consensus; Conradt and Roper, 2005). Peacekeeping by disrupting dyadic fights, a central feature of leadership in various social mammals (Beisner and McCowan, 2013) has the potential to elicit retaliation. In humans, costs of leadership include risk of injury in warfare (Beckerman et al., 2009; Glowacki and Wrangham, 2013), opportunity costs including reduced attention to tasks in which one is not a leader (Piyapong et al., 2007), and greater reputational damage from failed collective action as well as retaliation as a result of conflict mediation decisions (von Rueden et al., 2014). From an evolutionary perspective, as leadership in violent contexts, such as in warfare or intragroup peacekeeping, increases the exposure of leaders to bodily injury or death, female leadership is likely constrained by the centrality of mothers to offspring reproduction and survival (Kruger and Nesse, 2006; Campbell, 2013b). In order to minimize risk of injury, female primates in general may tend to engage in fights with greater selectivity than males (Clutton-Brock and Huchard, 2013b; Foerster et al., 2016).

Sexual Selection in Humans and Gendered Divisions of Labor

In non-industrial human societies, including egalitarian hunter-gatherers, men's leadership and other measures of social status (defined as a person's standing or importance in relation to other people within a society) tend to positively associate with various measures of reproductive success, particularly access to mates and fertility (von Rueden and Jaeggi, 2016). These effects are stronger in polygynous societies, where male leaders can marry multiple wives. In modern industrial societies, men's – but not women's – income tends to associate with greater fertility, but the relationship may be driven by poor men who fail to reproduce more than by greater reproduction of men at the top of the social hierarchy (Nettle and Pollet, 2008; Stulp et al., 2016). Associations of social status and leadership with reproduction among women has received less attention in non-industrial societies. However, existing studies suggest female status-seeking, in contrast to male status-seeking for leadership roles, may be motivated more by influencing decisions that improve child survival than by increasing mating opportunities (Alami et al., 2020). In general, available data suggest there tends to be greater variance in male compared to female reproduction within small-scale and large-scale human societies, though with considerable variation and in some instances a reversal of the gender difference (Brown et al., 2009; Betzig, 2012; Wilson et al., 2017). A comparison of mitochondrial and Y sequences from diverse human populations suggests the tendency for greater variance in male relative to female reproduction dates to before the migration of modern humans from Africa (Lippold et al., 2014), with particularly large decreases in the number of males (but not females) who reproduced in the wake of agriculture 5000–7000 before the present (Karmin et al., 2015). This sex difference in reproductive variance over historical and evolutionary timescales, coupled with evidence of gender-varying effects of leadership on reproductive outcomes, suggests that women and men may in general have evolved somewhat divergent though overlapping motivations for acquiring access to leadership positions.

Why one gender should consistently be more likely to emerge as an overt leader in human, mixed-gender community-level politics requires additional explanation. Our integrative perspective focuses on two general causes of gender differences in access to political leadership in human societies: (i) women and men tend to differ in how they compete and cooperate in the pursuit of leadership, and (ii) followers – regardless of their own gender – are often biased against selecting female leaders. Our view suggests that not only do both factors contribute to shaping observed patterns of leader emergence, but they influence each other. Sexual selection shapes gender-specific competition strategies, which in turn influence (but neither determine nor justify) cultural transmission of institutions and norms, such as women's and men's specialization in different forms of labor and expectations regarding gender-appropriate behavior. Institutions and norms can then feedback on gender-specific competition strategies. Moreover, this bidirectional exchange is moderated by socio-ecological conditions (see **Figure 2**), which can exacerbate or minimize gender differences in competitive strategies and shape the kinds of gendered divisions of labor that emerge. We develop these ideas below.

Gender biases in leadership access or preferences may emerge as a by-product of selection on other functions. Sexual selection has likely contributed to men's larger body size and strength (Lassek and Gaulin, 2009), and may continue to do so (Stearns et al., 2012). Upper body strength in particular is quite dimorphic in humans (Lassek and Gaulin, 2009). Sexual selection may also have contributed to a greater tendency among men for physical or other risk-taking behaviors when pursuing leadership roles (Wilson and Daly, 1985; Mishra et al., 2017) and a greater preference among men for direct aggression in dyadic or collective competition (Archer, 1988; Van Vugt et al., 2007). The greater contribution to women's reproductive success

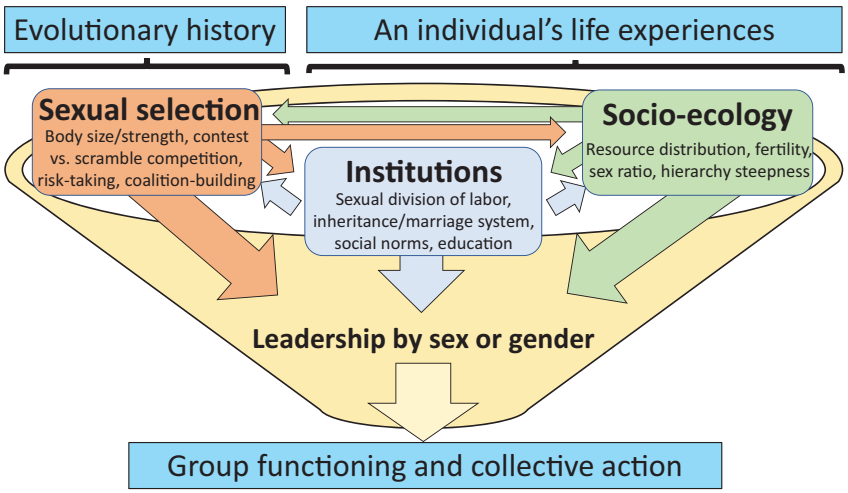

FIGURE 2 | Paths contributing to sex differences in leadership access and preferences. Sexual selection generates sex-specific traits, which interact with sociological circumstances over evolutionary history to generate institutional structures (humans) and traditions (non-human mammals). The effects of these processes on female access to leadership is mediated by learning over ontogeny, with consequences for group functioning and collective action. By recognizing these processes, as a cultural species, humans have the social flexibility and cognitive capacity to choose to confront and, to potentially overcome, sex-biased access to and preferences for leadership (Hrdy, 2009; Smith et al., 2020).

from parental investment, including gestation and lactation, may have made injury-causing activities riskier for women over human evolution (Campbell, 2013a). These risks may have contributed to a greater tendency among women to use indirect aggression, including gossip and social exclusion, in lieu of direct aggression to influence others (Hess and Hagen, 2006; Vaillancourt and Krems, 2018). Compared to women, men may have also experienced greater selection to engage in rapid, large-scale coalition-building, for purposes of often violent aggression (Wrangham and Peterson, 1996). Perhaps consistent with this claim is evidence, at least in WEIRD populations, that men can be more likely to build larger social networks with more "weak" ties (Vigil, 2007; Seabright, 2012; Friebel et al., 2017), prefer socializing in larger same-sex groups (David-Barrett et al., 2015; Benenson, 2019; Peperkoorn et al., 2020), and organize their groups hierarchically while revering other group members' competitiveness (Berdahl and Anderson, 2005; Watkins and Jones, 2016; Benenson and Abadzi, 2020). One general interpretation of the foregoing is that men and women may have evolved different, though overlapping, political strategies, where for men within-group cooperation may be more beneficial for enhancing between-group competition, while for women, within-group cooperation is likely to be more circumscribed and focused on recruiting sources of stable social support (Vandermassen, 2008; Mcdonald et al., 2012).

When they are present, these average gender differences in competition and cooperation may all have effects on gender differences in leader emergence. For example, average differences between women and men in risk-taking and preferred forms of competition may partly contribute to observations of a greater likelihood among men to self-promote and exaggerate competence in the pursuit of leadership (Chamorro-Premuzic, 2019), treat acquaintances or colleagues instrumentally to gain information, favors, or opportunities (Cullen-Lester et al., 2016), anticipate fewer risks to leadership (Sweet-Cushman, 2016), or be willing to make unilateral decisions on behalf of their group (Ertac and Gurdal, 2012). To the extent men more frequently socialize in large groups and build larger social networks with more "weak" ties, men may be advantaged in influencing the design of political institutions that regulate society and in accessing novel information or opportunities for ascending institutional hierarchies (Lindenlaub and Prummer, 2020).

Sexually selected strategies can also contribute to the evolution of follower psychology. For example, a contributing factor to favoritism for male leaders may be implicit or explicit associations between leader effectiveness and leaders' physical dominance. Experiments suggest group members show increased preference for physical dominance in leaders in contexts of negotiation or competition with other (out- groups; Lukaszewski et al., 2016; Laustsen and Petersen, 2017) or when conflict or free-riding is particularly threatening to within-group cooperation (Bøggild and Laustsen, 2016). Physically dominant leaders can pose their own threats to group members to the extent they lack other even more preferred traits in leaders such as expertise, fairness, and humility (Bøggild and Petersen, 2016), but the threat of group discoordination, dissolution, or extinction can loom larger. Even in democratic industrialized societies, references to body size are common to call attention to leaders' competence or lack thereof (van Vugt and Ahuja, 2011). For example, former United States president Trump's "broad-shouldered leadership" was a frequent refrain of his 2016 presidential campaign, which carried more than metaphorical meaning given the gender of his opponent (Chait, 2017).

Context-sensitive preferences for leaders with the capacity to wield physical dominance may have evolved for their functional value in the politics of small-scale societies lacking formal

legal and political institutions. Among the Tsimané forager-horticulturalists of Bolivia, a relatively egalitarian society, men's more overt influence over community politics is explained in part by their larger body size and strength, though to a lesser extent than men's greater exposure to formal education and greater number of cooperation partners (von Rueden et al., 2018). The body size effect may be due in part to perceived associations of body size with leader effectiveness (Kaplan et al., 2009; Blaker et al., 2013; von Rueden et al., 2014). Also, what predicts informal political influence in Tsimané women is similar to what predicts informal political influence in men: body size, access to education, social support, and their spouse's influence (von Rueden et al., 2018). Moreover, a study of recently settled hunter-gatherers in Ethiopia reached similar conclusions: gender is a weak predictor of community-level leadership once accounting for other predictors, and the traits that associate with men's and women's leadership are similar (Garfield and Hagen, 2020).

Furthermore, context can be critical for human gender differences in competition for leadership. Experiments have found that, cross-culturally, men tend to prefer even non-physical competitive situations more than women (Bönte, 2015), including in a highly egalitarian society (Apicella and Dreber, 2015). However, some studies in matrilineal contexts find no gender difference in preference for competition (Gneezy et al., 2009). Still other studies find that women can become as competitive as men when competition directly benefits their children (Cassar et al., 2016), when top performers are given the opportunity to share their winnings (Cassar and Rigdon, 2021), or when performance rankings are inconspicuous (Schram et al., 2019). These disparate results might be partly explained by evolved differences across women and men in the costs of losing competitions (Benenson and Abadzi, 2020; Cassar and Rigdon, 2021). Women may have evolved greater motivation to avoid loser resentment because of risks to allo-maternal support, particularly where kin support is less available.

Even more indirectly, a contribution of sexual selection to traits such as body size, risk-taking, competitiveness, and coalition building can create asymmetries that affect roles men and women take in terms of gender division of labor. The latter was precipitated over human evolution by ecological change that made humans increasingly reliant on energetically rich but difficult to acquire hunted and gathered foods (Kaplan et al., 2009; Alger et al., 2020). Humans evolved shorter inter-birth intervals and longer juvenile periods, in concert with increasing cooperation between pair-bonded sexual partners to care for and provision joint dependent offspring. How women and men have tended to contribute labor to the pair bond depends in part on sexually selected physiology and behavioral strategies. For instance, men tend to engage in more hunting compared to women across small-scale societies (Marlowe, 2005). Compared to other foraging strategies, hunting can be less compatible with pregnancy/lactation, is more compatible with men's greater tolerance for physical risk, can yield less consistent caloric returns for purposes of family provisioning, and provides more opportunities to show-off for building political influence and mate value (Hawkes and Bird, 2002; Gurven and Hill, 2009). The exceptions prove the rule: when women hunt in small-scale societies, it is typically with greater use of dogs and nets as opposed to upper-body strength intensive technology, and in pursuit of smaller, less riskily acquired game, which when shared is less conducive to showing-off but more for building cooperative support networks rather than gain mate value *per se* (Bird and Bird, 2008). Recent discovery of several early Holocene female skeletons associated with projectile point hunting technology raises the possibility that women engaged in more high-risk, large-game hunting in the past (Haas et al., 2020). If so, this must be reconciled with the infrequency of such hunting by women in recent small-scale societies.

Importantly, average differences in gender-specific behavior can emerge independent of coercion or discrimination and can then make it more likely that cultural norms stabilize gender-specific roles and punish deviance from them, reducing intra-gender behavioral variation (Micheletti et al., 2018). Furthermore, gendered divisions of labor and associated norms can feedback on the ability of women and men to pursue their optimal cooperation and competition strategies, such as by creating greater constraints on women's socializing beyond the household and on opportunities for acquiring wealth (von Rueden et al., 2018). Women in disparate small-scale societies may be more likely to gain political influence when they near menopause, perhaps because they have fewer childcare demands and are able to socialize more broadly within and beyond their communities (Brown, 1985). For example, women's group-level influence in the Mekranoti of the Brazilian Amazon negatively associated with their parenting demands (Werner, 1984), and there is evidence in the Tsimané that women's but not men's number of different cooperation partners negatively associates with number of dependent offspring (von Rueden et al., 2018). As previously described, introduction of the plow made agricultural labor more strength-intensive and less compatible with childcare, thereby decreasing women's labor value outside of the home, decreasing women's bargaining power, and decreasing women's access to leadership (Alesina et al., 2011). In another example, individuals from historically more pastoralist societies are more likely to promote restrictive norms concerning women's mobility (Becker, 2021). Econometric analyses suggest that men's fear of non-paternity due to periodic absence from their communities for herding or war initially promoted these restrictive gender norms (Becker, 2021). In other settings, economic opportunities may privilege women's work outside the home. Among Shodagor fisher-traders in Bangladesh, women travel to rural villages to trade with Muslim women, whose religion restricts their interaction with Shodagor men (Starkweather et al., 2020). In sum, gender division of labor likely acted as a key mechanism shaping the cross-cultural patterning of leadership by gender, phenomena that can only be fully understood through unification of evolutionary and social science approaches.

DEVELOPMENTAL ORIGINS OF SEX DIFFERENCES IN LEADERSHIP

A developmental perspective will help us to understand the ways that leadership roles are shaped across the lifespan by

sexually selected motivations and by cultural transmission of norms and institutions. In general, juvenile mammals tend to initiate collective movements less often and are less often involved in leading intergroup conflicts than adults (Fichtel et al., 2011; Majolo et al., 2020). In fish, followers are most likely to use social information from large (female) rather than small (male) demonstrators when making collective foraging decisions (Duffy et al., 2009). However, despite increased documentation that animals are selective in what, when and whom they copy (Kendal et al., 2018), we know little about how leadership and followership emerge across ontogeny in non-human animals.

Because individuals with high social rank in the dominance hierarchy may also impose a disproportionate influence in collective decision-making in some mammalian species (Van Vugt and Smith, 2019), understanding the mechanisms of dominance rank acquisition is also relevant and informative in this context. In many Old World monkeys, female dominance rank is determined by maternal rank inheritance, whereby daughters adopt the ranks below their mother in an age-reversed order (Harcourt and de Waal, 1992), but virtually all adult males, who acquire their rank based on size and strength, dominate all females (Pereira, 1995). In spotted hyenas, maternal rank inheritance is also implemented via this same associative learning of repeated social support from others (Holekamp and Smale, 1991; Vullioud et al., 2019), and high-ranking adult females emerge most often as leaders in resolving within-group conflicts, collective movements, and initiating intergroup conflicts (Boydston et al., 2001; Smith et al., 2010). In ring-tailed lemurs, female dominance over all males emerges spontaneously around puberty via male submission (Pereira, 1995). Thus, there exists great inter-specific diversity across mammals in the ways that socially powerful positions such as high dominance rank can be achieved. Similar patterns may apply to leadership emergence but will require explicit study.

In studies of children in WEIRD human societies, gender differences in social network attributes and group size preferences emerge early and perpetuate into adulthood (Rose and Rudolph, 2006; Benenson and Abadzi, 2020). For example, girls have been observed to have smaller same-gender play groups (Ladd, 1983; Ladd and Profilet, 1996) and less dense social networks than boys (Benenson, 1990, 1993). However, these trends can be strongly shaped by the preferences of a few popular youth who strongly favor boy companions; preferences for friends based on gender can be weak or absent for unpopular youth (Ladd, 1983). Furthermore, gender differences in social network size vary with age. A study of Europeans found that men have more social contacts than women, particularly in young adulthood, but then this gender difference reverses in middle age as the numbers of contacts for both genders precipitously decline and as reproductive priorities shift (Bhattacharya et al., 2016). In smaller-scale societies with higher fertility levels, women may tend to engage in more broad social networking as they approach middle age, perhaps because they have fewer dependent offspring in the household (Werner, 1984; Brown, 1985; von Rueden et al., 2018). In small-scale societies, children can be more likely to socialize in mixed-gender groups, which can weaken gender differences in behavior (Lew-Levy et al., 2019). A study of BaYaka and Hadza hunter-gatherer children finds that play within mixed-gender groups increases as the available pool of playmates decreases, and mixed-gender socialization may explain smaller gender differences in rough-and-tumble and other forms of play compared to WEIRD samples (Lew-Levy et al., 2019). Much more cross-cultural work is needed to determine variability in social networking and leadership emergence within networks by gender across the lifespan.

Gender differences in individual competitive behavior can also emerge early in development. Among young children, studies in WEIRD contexts find that boys tend to engage in more self-referencing behavior and are typically more likely to recognize and respect decision-making hierarchies within their groups, whereas girls are more likely to use indirect strategies, like ignoring, to compete for leadership positions (Hold-Cavell, 1996; Benenson and Abadzi, 2020). At older ages, the most popular children (both boys and girls) are the ones who apply tactics consistent with a combination of prestige and dominance leadership styles, though boys in general are more likely to pursue more purely coercive and aggressive tactics (Hawley, 2014). Gender differences in physical aggression and risk-taking may peak in late adolescence and young adulthood, when young men are most intensely competing to establish mate value (Wilson and Daly, 1985). Young women tend to compete more than men by emphasizing aspects of their physical appearance that signal residual reproductive value to potential mates (Cashdan, 1998; Campbell, 2013b).

Importantly, gender differences in social network building and in competition for leadership positions are shaped by norms of expected behavior (e.g., greater encouragement of boys to engage in team sports or girls to assist in childcare). Cross-culturally, manhood more than womanhood is described as something to be earned, and which can be gained or lost depending on display of competitive ability, skill, generosity, and leadership (Vandello et al., 2008). Societies that experience greater intergroup conflict are more likely to portray manhood as precarious in this way, and to impose costly initiation rites of passage on young men to test their manhood (Sosis et al., 2007) due to benefits to male coalition building in the context of war (Rodseth, 2012). These norms may also reflect evolved, gender-specific motivations, but, obviously, they are not determined by them (Henrich, 2015). For example, the more that prestigious political positions in society are monopolized by men, the more they may be likely to promote norms and build institutions that exacerbate and canalize average gender differences in competition, coalition-building, or even desire for political leadership.

Follower preferences in leaders also emerge early and can change over the lifespan. Even infants possess the ability to distinguish between bullies and leaders (Margoni et al., 2018). Harsh childhood conditions may favor long-lasting preferences for dominant-style leaders that rely upon the threat of punishment (Safra et al., 2017). Follower preferences may have effects on gender disparity in leadership well before aspiring leaders reach adulthood. In the United States, one study found that adolescent girls showed less ambition as political leaders than adolescent boys, likely in part because boys were more likely to

be groomed and described as prospective leaders, by their family members, teachers, coaches, and other role models (Lawless and Fox, 2013). A recent study found no gender difference in interest in being a leader among 3- to 7-year-old children, but girls were less likely than boys to pick a same-gender peer as a leader (Mandalaywala and Rhodes, 2021). Like any social phenomenon, such favoritism toward boys is unlikely to be purely a social construction, but rather shaped by a complex interplay over evolutionary and historical timescales of evolved motivations with cultural transmission of institutions and norms, particularly a gendered division of labor.

INTEGRATING EVOLUTIONARY AND SOCIAL SCIENCE PERSPECTIVES

There are many benefits to viewing female leadership within a transdisciplinary perspective that integrates evolutionary and social science perspectives (Kappeler et al., 2019; Smith et al., 2020). Social role theories of gender (Eagly and Karau, 2002) are often contrasted with sexual selection approaches to gender differences, but we argue that these perspectives are not incompatible. More specifically, we focused on two outcomes of the mutual influence of evolutionary, ecological, and cultural factors, which often act to constrain female political leadership. That is, female competition and cooperation in pursuit of leadership can differ on average from that by males, and followers often demonstrate preferences for male over female leaders. As discussed above, evolved trait differences in humans can help explain the emergence and persistence of institutions and cultural norms, which enforce greater behavioral similarity within genders, affect opportunities for leadership by gender, and shape stereotypical conceptions of leadership. Emergence of particular gender norms and gender differences in leadership are further contingent on historical and cross-society variation, in subsistence, in inheritance systems, and in other factors. Studies in more egalitarian hunter-gatherers and other small-scale societies often report women exercising considerable leadership via inter-individual conflict resolution and criticism of non-normative behavior, though women can be less likely than men to coordinate community-wide activities and men's voices can be more numerous during community political discussions (Collier and Rosaldo, 1981; von Rueden et al., 2018; Garfield et al., 2019). The agricultural revolution was a principal influence on historical increases in political inequality and exacerbation of patriarchy (Kaplan et al., 2009; Mattison et al., 2016; Van Vugt and Smith, 2019; von Rueden, 2020). This is partly due to the effects of agricultural innovation on gendered divisions of labor that further privileged men's social networking and access to wealth (Coontz and Henderson, 1986; Alesina et al., 2011) and to increased incentives for male coalition-building in the face of more frequent warfare (Hayden et al., 1986; Rodseth, 2012). While women were more likely to hold formal political positions in those agricultural societies with matrilineal descent (Low, 1992), women's leadership positions tended to be less numerous or less powerful than their male counterparts (Whyte, 1978). Men continue to hold more top positions of formal leadership in large-scale, industrialized societies, but this gender gap has decreased in recent decades where ecological and economic conditions promoted declines in fertility and shifts in norms concerning women's education and labor force participation (Konner, 2015). There is evidence in WEIRD societies of large decreases in stereotypical associations of masculinity with competence and with leadership (Koenig et al., 2011; Eagly et al., 2019) and a decrease in preference for male over female bosses (Brenan, 2017). The balance of political power between women and men is shaped by the interplay of evolved gender differences, socio-ecology, and changing cultural institutions and norms (Low, 2005).

Our comparative perspective elucidates that overt forms of political decision-making are only one way in which individuals exert leadership in collective group decisions. In many mammalian species, females often emerge as leaders in the context of group movement for foraging or danger avoidance, less via active communication than by moving first (Smith et al., 2020). In small-scale human societies, men's politics may tend to be more public and aggrandizing but women frequently exert influence at the community level via less conspicuous means (Rosaldo, 1974). In a study of Tamil communities in south India, women were less likely than men to be identified as politically influential, partly because of less access to formal employment or material wealth. However, Tamil women may yield influence that is less visible through the more numerous support relationships they foster between community members (Power and Ready, 2018). In many human societies, men's historical monopolization of formal political leadership has contributed to associations of "appropriate" leader qualities with forms of competition more often preferred by men (Rudman and Phelan, 2008; Hoyt and Burnette, 2013). In addition to calling attention to gender inequality in overt forms of political leadership, scholars should devote more attention to more subtle forms of leadership displayed by women (and men) that can be as or more relevant to collective decision-making in human societies.

SOME IMPLICATIONS FOR POLICY

Increasing returns to education in a more globalized, service-oriented economy may be increasing the rewards to women's preferred strategies to acquire leadership. Women now outpace men in educational attainment and life satisfaction in many of the most economically developed societies (Stoet and Geary, 2019). However, gender inequality in access to leadership positions in business, government, and other sectors persists. Consideration of the linkages between evolution and cultural norms provides a more comprehensive toolkit for dismantling contemporary gender inequality in access to top leadership roles. We offer five policy-relevant suggestions, which are neither the only ones that could follow from our integrated framework, nor necessarily what other evolutionary-informed approaches suggest.

First, we may be unlikely to generate gender equity in leadership largely by promoting behavioral similarity in women and men, such as simply encouraging women to "lean in"

(Sandberg, 2013). Even in the absence of negative evaluations of women leaders who violate existing gender norms (Rudman and Phelan, 2008; Hoyt and Burnette, 2013), women and men, on average, may be motivated to pursue different leadership styles, with women, on average, adopting a more democratic, relational style (Eagly and Johnson, 1990; van Engen and Willemsen, 2004). A contribution of sexual selection to gender differences in competition and cooperation suggests average differences in leadership style are unlikely to universally disappear, but rather may be moderated by norms and institutional settings that change the gender-specific costs and benefits to particular forms of competition and cooperation (Gneezy et al., 2009; Cassar and Rigdon, 2021). Across societies, increased gender equity may even associate with increased (not decreased) average gender differences in many values and motivations (Falk and Hermle, 2018) – a phenomenon known as the gender equality paradox (Stoet and Geary, 2019, but also see: Breda et al., 2020). However, inter-individual variation independent of gender has and will likely continue to eclipse any average gender differences in predicting leader behavior (Bass and Stogdill, 1990).

Second, we can limit the extent to which certain gender differences privilege male leaders by calling attention to their limited or even negative impact on leader effectiveness. This includes men's greater tendency for self-promotion, overconfidence and exaggerating their competence, which helps elevate many unqualified men to positions of power (Chamorro-Premuzic, 2019). To the extent men, more than women, prefer to socialize in larger same-sex groups (Low, 1992; David-Barrett et al., 2015; Benenson, 2019; Peperkoorn et al., 2020) and to build larger social networks comprised of many "weak" ties (Vigil, 2007; Seabright, 2012; Friebel et al., 2017), men may be unduly privileged in the pursuit of leadership, particularly in the mixed gender hierarchies of large organizations (van Vugt and Spisak, 2008; Cullen-Lester et al., 2016; Lindenlaub and Prummer, 2020). Effects of social networking on gender differences in leadership are exacerbated when leaders tend to be male and leaders in general prefer to hire and promote similar others (i.e., the "old boys network") (McDonald, 2011; Koch et al., 2015). We should scrutinize the extent to which organizations reward men's more than women's preferred forms of competition and cooperation (Cassar and Rigdon, 2021). Not just to redress inequality in leadership access, but also because organizational goals can suffer when competitive ("toxic") masculinity dominates an organizations' culture (Berdahl et al., 2018). We can also call attention to implicit preferences regarding leaders' physical formidability and dominance (Blaker et al., 2013), and the ways in which the media and politicians stoke fear of out-groups (Lopez, 2020) to draw out these preferences. Studies with WEIRD participants find male leaders are preferred during war whereas preferences for female leaders increase during times of peace (Van Vugt et al., 2007; Grabo and van Vugt, 2018; de Waal-Andrews and van Vugt, 2020).

Third, we can make use of other evolved motivations, particularly our tendency to emulate prestigious role models (Jiménez and Mesoudi, 2019), to chip away at cultural norms favoring men in positions of leadership. The more often that existing leaders, men or women, promote women as leaders, the more we normalize women as leaders and change stereotypical associations of leadership with masculinity. In a now famous study in India in which villages were randomly assigned a requirement to elect women as chief councilors, girls in the villages were subsequently more likely to aspire to higher education and politics (Beaman et al., 2012) and men acquired more positive views of women's leadership ability (Beaman et al., 2009). Institutional requirements for gender equity and inclusion can be transformational in shaping male and female preferences and female access to leadership.

Fourth, organizations can accelerate cultural change in gendered divisions of labor by making work more compatible with childcare and by adopting more charitable parental leave policies. Expansion of paternity leave can boost men's contribution to childcare and housework long after the period of paternity leave (Buenning, 2015; Patnaik, 2019). While women and men may differ on average in preferred work-childcare tradeoffs, such tradeoffs can be highly contingent on not only cultural norms and institutions but also on the biological changes that can accompany fatherhood. Parenthood can decrease men's desire to compete and advertise mate value as suggested by cross-cultural evidence that reductions in testosterone can follow new fathers' direct involvement with their children (Gray et al., 2006; Gettler et al., 2011).

Fifth, societies can benefit by harnessing the diversity of leadership styles that come with a more equitable mix of female and male leaders. While average sex differences in preferences and motivations do not tend to be very large (Archer, 2019), they can still have important effects. In certain contexts, leader effectiveness may hinge more on risk-seeking, overt competitiveness, and creation of rigid hierarchical coalitions, on average favoring male leaders. In other contexts (Post, 2015), and some argue the majority of contexts (Eagly et al., 2003; Konner, 2015), leader effectiveness may hinge more on less direct forms of competition, risk aversion, and more empathy-driven forms of relationship building, on average favoring women leaders. For example, a study of gender quotas for firms in Norway found that more female directors decreased a firm's shorter-term financial performance but also decreased exposure to risk, with potentially longer-term positive consequences (Yang et al., 2019). In addition, women leaders can be more likely to prioritize issues like healthcare, welfare, and education (Funk and Philips, 2019; Hessami and da Fonseca, 2020) that advantage the most disadvantaged in society. Moreover, women's empowerment in general may be a key driver of transitions to greater democracy and transparency in government, and, in some cases, promote better outcomes during times of crisis (Wyndow and Mattes, 2013; Coscieme et al., 2020; Windsor et al., 2020).

AUTHOR CONTRIBUTIONS

All authors contributed the ideas and the writing of this manuscript.

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Third-Party Perceptions of Male and Female Status: Male Physical Strength and Female Physical Attractiveness Cue High Status

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Status is a universal feature of human sociality. A lesser-studied adaptive problem surrounding status is assessing who has which levels of status in a given group (e.g., identifying which people possess high status). Here, we integrate theory and methods from evolutionary social science, animal behavior, and social psychology, and we use an emotion inference paradigm to investigate what cues render people high status in the eyes of social perceivers. This paradigm relies on robust associations between status and emotion display—particularly the anger display. If a target is expected to enact (but not necessarily feel) anger, this would suggest that social perceivers view that target as higher status. By varying target attributes, we test whether those attributes are considered status cues in the eyes of social perceivers. In two well-powered, pre-registered experiments in the United States (N = 451) and India (N = 378), participants read one of eight vignettes about a male or female target—described as high or low in either physical strength or physical attractiveness (possible status cues)—who is thwarted by another person, and then reported expectations of the target's felt and enacted anger. We find that people expected physically stronger (versus less strong) men and more (versus less) physically attractive women to enact greater anger when thwarted by a same-sex other. Strength had no significant effect on estimations of female status and attractiveness had no significant effect on estimations of male status. There were no differences in expectations of felt anger. Results suggest that people use men's strength and women's attractiveness as status cues. Moreover, results underscore the notion that focusing on male-typical cues of status might obscure our understanding of the female status landscape. We discuss how this paradigm might be fruitfully employed to examine and discover other unexplored cues of male and female status.

Keywords: status, evolutionary social science, sex/gender differences, social perception, emotion

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INTRODUCTION

Status confers fitness benefits because group members allow high-status individuals to receive relatively unchallenged or preferential access to contested resources (e.g., Anderson et al., 2001; von Rueden et al., 2011; Majolo et al., 2012; Cowlishaw and Dunbar, 2021). Such status exists in the eyes of beholders. The central, related question we explore here—one considered relatively overlooked

in this area of research (Buss et al., 2020)—focuses on the adaptive problem that beholders face in identifying who has high status. Specifically, at zero acquaintance, what cues lead us to infer that a target is high status?

The first features that might come to mind are likely a target's significant physical strength, great riches, or political positions. The perceptually salient instantiations of these features (e.g., big muscles, expensive watches) are indeed thought to be associated with status (von Rueden et al., 2008, 2014; Blaker and van Vugt, 2014; Lukaszewski et al., 2016; Buss et al., 2020; Durkee et al., 2020). Here we suggest that, although correct, the primacy of these features might suggest an implicit bias in some social science work whereby researchers have privileged male-typical defaults for cognition and behavior. Put differently, when people—researchers and laypeople alike—think about status features, we often think first about features that reliably augment *men's* status. Nevertheless, some features that render men high status are likely distinct from some of those that render women high status (e.g., Rucas, 2015; Buss et al., 2020).[1] Thus, the cues that evoke perceptions of male high status might not "work" for women. Likewise, those cues that evoke perceptions of female high status might not "work" for men.

Here, we explore which target features cause social perceivers to view men and women as possessing high status. To this end, we leverage robust associations observed in previous research between anger and status—that relatively higher status people display anger more often, and that social perceivers expect relatively higher status people to display anger more often (Tiedens et al., 2000; Hess et al., 2005; Hareli et al., 2009; Sell et al., 2009, 2017). Concretely, we explore whether United States and Indian social perceivers infer more (versus less) physically strong men and physically attractive women to be more likely to display anger when thwarted by a same-sex/gender other. If so, these anger expectations would imply that United States and Indian social perceivers use men's physical strength and women's physical attractiveness as cues to those targets' high status. This work thus integrates prior research on status, sex/gender, and emotion stereotyping to test basic predictions about which features influence status perceptions. Additionally, it introduces a useful experimental paradigm for the further investigation of additional and perhaps understudied status features.

STATUS

Hierarchies are common across the animal kingdom. So, too, are instances of some animals being closer to the top of those hierarchies and thus enjoying preferential access to contested resources and the fitness benefits this generates (e.g., Noë et al., 1980; Wasser and Barash, 1983; Sapolsky, 2004; Smith and van Vugt, 2020). Such status hierarchies also exist across human cultures, from industrialized to small-scale societies (e.g., Brown, 1991; Boehm, 1993; von Rueden et al., 2008, 2011; Anderson et al., 2015). Therein, higher relative status position seems to reliably foster improved fitness outcomes, although this seems to be most well-studied and clear among males. For example, in small-scale societies, men's high status is associated with better health outcomes and privileged access to resources; and in data from 33 non-industrial societies, male status (as indexed by wealth and political influence) positively predicts the number of men's surviving children (e.g., Berger et al., 1980; Patton, 2000; von Rueden et al., 2011, 2019; von Rueden and Jaeggi, 2016[2] (for some status-fitness links among females, see Bowser and Patton, 2010; Rucas, 2015; Alami et al., 2020). This link between one's own high status and increased fitness underscores a prominent adaptive problem surrounding status: How does one attain it?

Another important challenge is discerning who has higher (and lower) status. Indeed, consider the useful things you can do if you know the relative status of each fellow group member: demanding deference from lower-status individuals (or coalitions), punishing non-deference by lower-status individuals, deferring to higher-status individuals, taking courses of actions aimed at enhancing the status of self and associates (e.g., offspring; Scelza, 2010), and so on. A basic requirement to do these things is the ability to estimate, or compute, the social status of a given individual relative to that of self (and specific others) (e.g., Henrich and Gil-White, 2001; Buss et al., 2020).

But discerning someone's status is no easy task. The status of an unacquainted individual is neither necessarily known nor immediately accessible. People do not walk around with their status levels emblazoned on their chests (e.g., "I am a 10/10 on status in this group"). Rather, someone's status must be inferred from perceivable cues and lower-level inferences (e.g., association with someone already known to have high status, ownership of a Ferrari).

To make this discernment, people should track cues that are reliably linked to being valued because they generate benefits and/or inflict costs in a given environment (Foulsham et al., 2010; Blaker and van Vugt, 2014; Durkee et al., 2020)[3]. For example, ancestrally, objects (e.g., food), personal characteristics (e.g., ambitiousness), physical characteristics (e.g., size), relational characteristics (e.g., having allies), emotional expressions (e.g., the anger expression), and so on may have had characteristic associations and effects on people's status, on average. If so, the mind may be designed to estimate a target's status by tracking a wide array of potentially status-relevant features (e.g., the value of the objects owned by the target, the kinds of emotions expressed by the target in a given context). To illustrate, the modern mind might use Tom's frequent driving of a Ferrari to produce the inference that Tom *owns* the Ferrari and the additional inference that Tom has overall high status in his community.[4]

[1]This same logic also necessarily implies that some of the features that render people high status in the eyes of others are the same for male and female targets.

[2]Jaeggi, A. V., Blackwell, A. D., von Rueden, C., Trumble, B., Stieglitz, J., Garcia, A., et al. (under review). Relative wealth and inequality associate with health in a small-scale subsistence society. *medRxiv* [Preprint]. doi: 10.1101/2020.06.11.2012 1889

[3]Sznycer, D. (under review). Human values: a cognitive perspective. *PsyArxiv* [Preprint].

[4]Further, status is necessarily relative; the status level of any one target critically depends on which other individual(s) the target is compared against (e.g., I might view Tom as having higher status than Ben because Ben drives a Toyota, but as having lower status than Joel because Joel drives a custom Bugatti). Moreover, status is an n-person-coordinated social construct (e.g., *I* may be under the impression that Tom has high status because of his Ferrari, but everyone else in the

So, what are the cues that people attend to in attempting to discern if an unknown man or woman is high status?

Status Features

"[R]elatively little is known about the precise criteria by which humans assess and allocate status" (Buss et al., 2020, p. 980). Indeed, conceivably, there could be myriad features that render a target high status. If status cues were arbitrary, anything could be or become one. From an adaptationist view, however, features that contribute to perceptions of high status will often be non-arbitrary; they will often be features that would have rendered a target better able to generate benefits for and/or inflict costs on other group members (e.g., features that render a target a better ally, leader, mate, friend, advisor, hunter, caretaker, and a more formidable rival). But consider that what makes a person a good ally or a dangerous rival might differ depending on that person's sex/gender, one's own sex/gender, one's culture, and so on. Indeed, the expectation is that status cues will often vary with respect to various perceiver and target identities and relationships, as well as across cultures, subcultures, and so on. Here, we focus on the influence of target sex/gender on status cues and on two of the most likely sex/gender-differentiated status features: male physical strength and female physical attractiveness.

Male Physical Strength

For researchers and laypeople alike, many of the features that immediately come to mind as cueing status might be especially reflective of men's abilities to garner access to contested resources. One reason for this is because status and resource access among non-human animals is often determined by success in agonistic conflicts, which itself is often determined by an individual's size and strength (e.g., Chase and Seitz, 2011; Bush et al., 2016; Holekamp and Strauss, 2016). Among humans, however, there are multiple routes to status (e.g., Cheng et al., 2013; Redhead et al., 2019).

This is not to suggest that features boosting a *person's* likelihood of success in agonistic physical conflicts are ignored in status estimations (see, e.g., Buss et al., 2020; Durkee et al., 2020; Chen Zeng et al., 2022). In fact, given the long history of male coalitional hunting and raiding—in which success would have been enhanced by physical formidability (among other features)—one might expect the social mind to use men's physical strength as a status cue (e.g., Sell et al., 2009; Buss et al., 2020). In fact, social perceivers are known to use a man's size and strength as cues to his status (e.g., Blaker and van Vugt, 2014; Lukaszewski et al., 2016; Durkee et al., 2018; Buss et al., 2020; von Rueden, 2014; von Rueden et al., 2008, 2014). Moreover, more physically formidable men are expected—by themselves and by others—to receive greater deference and consideration from others (e.g., Sell et al., 2012; Lukaszewski, 2013; Delton and Sell, 2014; Pietraszewski and Shaw, 2015). Note that this need not be solely because stronger men can more effectively take contested resources or inflict costs on those who obstruct access to them (e.g., Sell et al., 2009, 2012, 2016). This same status conferral can also owe to strong men's abilities to generate benefits to their allies and other group members (e.g., Eisenbruch et al., 2016; Lukaszewski et al., 2016; Stavans and Baillargeon, 2019; Durkee et al., 2020).

To the extent that men's physical strength contributes to estimations of their physical attractiveness, it is possible that more attractive men might be inferred to have higher status (e.g., Lukaszewski et al., 2016; Sell et al., 2017). These men are at least inferred to have greater access to desirable mates (Brown et al., 2021). However, male attractiveness also does not predict allocations of status when controlling for male strength (Lukaszewski et al., 2016).

Female Physical Attractiveness

Women's size and strength may not be straightforwardly linked with expectations of their greater consideration (in their own or in others' eyes). Given both the relative lack of female coalitional warfare and also women's comparatively lower preferences of using physical aggression (e.g., Burbank, 1987; Campbell, 1999; Vaillancourt, 2013), female physical size and strength may not have been hugely beneficial. Indeed, some have asserted that physical aggression could threaten a woman's ability to bear or care for offspring, hence women's lesser use of it (Campbell, 1999; see also Griskevicius et al., 2009). Further, given the size asymmetries imposed by sexual dimorphism, even great sex-typical strength would leave most females unable to win physical contests against most males (e.g., Puts, 2010).

Rather, some have reasoned that physical attractiveness should be one cue of women's status (e.g., Buss et al., 2020; see also Sell et al., 2009). This view is premised on the long evolutionary history of physical attractiveness being (a) central to female mate value and (b) reflective of the fertility benefits women could confer (or withhold). Others have also extended this notion, suggesting that physical attractiveness can render women desirable social partners for relationships beyond (heterosexual) mating ones (e.g., Eisenbruch and Roney, 2020). And still others have noted that some of the benefits girls and women glean if they are considered physically attractive—access to higher quality social and romantic partners, greater access to resources, more social attention and influence—help females attain other aspects of status that might then lead people to defer to those women and also associate women's physical attractiveness with the presence of additional status features (e.g., attention, popularity) (e.g., Vaillancourt and Krems, 2018; Fisher and Krems, in press; Bradshaw and DelPriore, 2021)[5].

EMOTION AND STATUS: THE CASE OF ANGER

Emotions and status are tightly intertwined (see, e.g., Tiedens, 2001; Shariff and Tracy, 2009; van Kleef and Lange, 2020; Durkee, 2021). For example, adaptationist views suggest that pride tracks status gains and motivates individuals to garner greater valuation and respect from others (e.g., Sznycer et al., 2017, 2018b; Durkee et al., 2019; Cohen et al., 2020; Sznycer and Cohen, 2021).

community sees his new Ferrari as parvenu, deeming him low status and treating him accordingly.

[5]Krems, J., Hahnel, R., Merrie, L. A., and Williams, K. (under review). Sometimes we want vicious friends: friend preferences are target-specific. *PsyArXiv* [Preprint]. doi: 10.31234/osf.io/4fjx8

Likewise, shame tracks status losses and motivates individuals to mitigate their status losses (e.g., Sznycer et al., 2012, 2016, 2018a; Durkee et al., 2019; Cohen et al., 2020). Here, we focus on the emotion of anger and its links to a target's status.

An adaptationist view of anger sees it as a recalibrational emotion designed to motivate a person to bargain for better treatment from others (e.g., Sell et al., 2009, 2017). On this view, my anger is evoked when another person places insufficient weight on my welfare relative to what I feel entitled to (based on our relative bargaining power). I should feel angry when I feel undervalued (Sznycer and Lukaszewski, 2019). Of course, anger is not the only emotional display that might be plausibly recruited in this situation; less explored is the notion that people might enact crying, whining, and other need-signaling tactics to bargain for better treatment (in the context of communal relationships). But anger, specifically, is theorized to be implemented when individuals with greater ability to inflict costs on or to withhold benefits from others feel undervalued (Sell et al., 2009, 2017; Sznycer and Lukaszewski, 2019).

A definitional component of having high status is that others acquiesce to one's will; one also has greater influence over others and priority access to contested resources. Thus, relative to lower status people, a higher status individual should have greater ability, for example, to inflict reputational costs on someone who undervalues them (e.g., influencing others to think negatively about the undervaluing target), and/or to withhold benefits from someone who undervalues them (e.g., forestalling the undervaluing target's ability to access food or desirable partners). The recalibrational view thus predicts that people with greater ability to inflict costs on or withhold benefits from others (i.e., higher status people) should be more anger prone, have a greater sense of entitlement, and perhaps report a richer history of using anger-based aggression to get their way.

Importantly, evidence suggests that these predictions are correct (e.g., Sell et al., 2009, 2016, 2017; van Kleef and Lange, 2020; Durkee, 2021)[6]. For example, Sell et al. (2009) found that physically stronger men (presumed to have greater ability to inflict physical costs on others) and physically attractive women (presumed to have greater reproductive potential that they can withhold) reported greater anger proneness.[7] Moreover, anger displays may also be more effective for such individuals (Sell et al., 2009). This is not to say that higher-status people necessarily feel greater anger. Higher-status people might have lower thresholds for anger feelings and be quicker to feel anger—or not. Regardless, many higher-status people often seem to be less likely to inhibit their overt displays of anger and are more likely to enjoy greater freedom to express that anger (e.g., Sell et al., 2016; van Kleef and Lange, 2020; Durkee, 2021). So it is possible, for example, that both higher- and lower- status people experience similar levels of anger at being thwarted, but higher-status people are simply more likely to overtly display that anger (and achieve its recalibrational ends).

Moreover, not only are higher-status people perhaps more likely to display their anger when undervalued, but social perceivers have picked up on this relationship between anger display and status. For example, some work in social psychology has explored emotion stereotypes—social inferences about who is likely to show what emotions (e.g., Tiedens et al., 2000; Tiedens, 2001). One line of this work has shown that social perceivers use emotional displays to make inferences about displayer status (e.g., Hareli et al., 2011; Mast and Palese, 2019). In particular, social perceivers reliably and bidirectionally associate a man's or woman's high status with their likelihood of displaying anger (e.g., Knutson, 1996; Tiedens et al., 2000; Tiedens, 2001; Hess et al., 2005; Hareli et al., 2009). Somewhat similar to the recalibrational theory (for actors), some social psychological work based in appraisal theory holds that, in the eyes of perceivers, anger is associated with social power because it leads to appraisals that anger-expressing actors are able to control and influence their social environment (Keltner et al., 2003; Lerner and Tiedens, 2006). Indeed, people are often perceived to be of higher status when they display anger (versus other emotional expressions) (Aguinis et al., 1998; Tiedens, 2001), and higher-status people are expected to display more anger when their goals are thwarted (Tiedens et al., 2000; Hess et al., 2005; Hareli et al., 2009).

One might wonder, however, how such a relationship—whether genuine or perceived—between anger display and status could exist. For example, if social perceivers can easily infer someone's status from perceptually salient cues, one might wonder why perceivers would ever treat a high status person in a way that undervalues them and evokes their anger (and thus there should be no relationship between status and anger but rather only a relationship between status and appeasement).[8] There are several possible reasons that people might undervalue, in the target's eyes, high-status targets. First, one might not realize that their actions communicate undervaluation, perhaps because the consequences of those actions are opaque. Second, the target of

[6]Tiedens, L. Z., Ellsworth, P. C., and Moskowitz, D. S. (1998). *Feeling Your Place: Emotional Consequences of Social Status Positions.* Unpublished manuscript.

[7] Note that higher-status people might not always display anger in the ways that first come to mind. For example, a strong man might get in the face of a weaker man who undervalues him, a more traditional conceptualization of anger, and perhaps one especially linked to status based on dominance or cost-infliction. Such strong men might also be more likely to have outbursts of anger unpredictably (i.e., not only in reaction to being undervalued; Cheng et al., 2010). The same behavior would be taboo in a faculty meeting, however, even if an ostensibly lower-status adjunct undervalued a seeming higher-status full professor; and the same behavior is less likely to be observed among women, who might be more likely to hide their anger and later engage in forms of indirect aggression that allow the aggressor to remain anonymous (see Krems et al., 2015; see also Brescoll and Uhlmann, 2008). These brief examples suggest that anger displays from those who derive status from prestige or benefit generation (and withholding; for reviews see, e.g., Maner, 2017; Cheng, 2020; see also Case et al., 2021) might be less likely to engage in overt and perhaps male-typical anger displays (i.e., anger displays as traditionally conceptualized). If this is the case (e.g., Henrich and Gil-White, 2001; Case et al., 2021), it suggests that we first need to better understand what features are linked to perceptions of cost infliction and benefit generation, for which perceivers, and in which situations; from there, we might derive better informed predictions about the efficacy of using different modes of anger-based aggression (e.g., direct, indirect) toward recalibrational ends.

[8]One could easily ask a seeming inverse of this question as well: What is to stop a person from making an anger expression and/or enacting anger all of the time to reap the benefits of being perceived as higher status? One reason people might not do this is because interpersonal anger might be ineffectual, if not exceedingly costly, for actors who are unable to back their anger up with the ability to inflict costs or withhold benefits.

one's actions might be unknown. To illustrate, I might buy the café's last almond croissant without realizing that a higher-status person was maneuvering for it. Third, there could be situations in which the norms are *not* based around highest bargaining power leading to greatest influence—for example, norms wherein each person gets an equal vote, regardless of bargaining power. Enforcement of such a norm would comparatively disadvantage those with higher status and potentially anger them.

THE PRESENT WORK

Here, we leverage these robust associations between anger and status—that social perceivers expect higher-status people to display more anger when thwarted—to explore what some status-cueing features might be. And we use a potentially effective new paradigm for identifying which features social perceivers use to infer target status. Specifically, we ask if United States (Experiment 1) and Indian (Experiment 2) social perceivers infer: (1) physically stronger (versus weaker) men to display greater anger when thwarted by another man; and (2) more (versus less) physically attractive women to display greater anger when thwarted by another woman. If so, these anger expectations would imply that social perceivers use male physical strength and female physical attractiveness as cues to those respective targets' high status. In other words, by experimentally manipulating the types and levels of two plausibly status-connoting attributes, and then asking social perceivers to infer the level of anger displayed when people possessing these attributes are thwarted, we aim to gain insight into how the mind determines the status of unknown men and women.

Experiments 1 and 2 test these predictions in the United States and in India, respectively. Preregistrations, data, and syntax are available on Open Science Framework: https://osf.io/u4rcj/.

EXPERIMENT 1 (UNITED STATES) AND EXPERIMENT 2 (INDIA)

Methods

Participants

Experiment 1

We aimed to collect usable data from 450 United States adult community participants. Of 563 who at least began our short survey on CloudResearch, 451 (263 female; M_{age} = 41.45, SD_{age} = 13.18) passed a bot (having Qualtrics' reCAPTCHA score $\geq$ 0.4) and two attention checks (e.g., "Please set the bar to 100 if you are paying attention") and reported their sex. This yielded 0.80 power to detect small effects (f ~0.13).

Experiment 2

We aimed to collect usable data from 450 Indian adult community participants. Of 557 who at least began our short survey on CloudResearch, 378 (116 female, 2 other; M_{age} = 31.08, SD_{age} = 8.33) passed a bot (having Qualtrics' reCAPTCHA score $\geq$ 0.4) and two attention checks (e.g., "Please set the bar to 100 if you are paying attention") and reported their sex. This yielded 0.80 power to detect small effects (f ~0.14). We had previously planned to additionally exclude those participants failing a fill-in-the-blank, open-ended English comprehension check ("Eagles, hawks, sparrows, and robins are all examples of what kind of animal?"); given that excluding those failing that check would restrict our sample size to 314 (96 female, 2 other) but would not change the patterns of results, we chose to include those participants failing this check in the results reported below.

Design and Procedure

Both experiments shared a 2 (Target gender) × 2 (Attribute) × 2 (Level of Attribute) between-subjects design. Participants were thus randomly assigned to read one of eight short scenarios about a man or woman on their way home from a long day at their office, heading to the bus stop. They have not eaten all day and stop to buy food near the bus stop. But while waiting to check out, a same-gender stranger cuts in front of them in line (see Sell et al., 2017); this stranger thus causes the target to miss the bus and wait in an undesirable area of town for an hour until the next bus arrives.

In the start of each vignette, the target was described as being high or low in physical strength or physical attractiveness compared to same-gender others. See **Appendix A** for vignettes.

Participants were then asked to report their inferences about how the target would feel ("Based on the scenario you just read, to what extent do you think that Alex would FEEL on the INSIDE. . .") and act (". . .ACT on the OUTSIDE") toward the person who thwarted their plans (i.e., cut in front of them in line, forcing them to wait for the next bus) using two 100-point sliders (*0 = not at all*, *100 = very much*). Embedded among seven total items were two focal items assessing our focal dependent variable of anger ["angry at the (man/woman) in line", "annoyed. . ."; $\alpha_{feelings}$ = 0.73–0.85; $\alpha_{actions}$ = 0.84–0.88]; other items were grateful ("grateful to. . .", "appreciative of. . ."), sad ("sad. . ."), and surprised ("surprised. . ."), and were not included in analyses. Items appeared in randomized order, as did blocks assessing inferences of feelings and displays.

RESULTS

Experiment 1

In the United States sample, we conducted a 2 (Reaction: Feelings, Actions) × 2 (Target sex/gender) × 2 (Attribute: Physical Strength/Attractiveness) × 2 (Level: High/Low) mixed-factors Analysis of Variance (ANOVA) to explore people's expectations of targets' angry feelings and actions in response to being thwarted by a same-sex/gender stranger.[9] In light of a significant four-way interaction, $F(1,443) = 9.48$, $p = 0.002$, $\eta_p^2 = 0.021$, we first examined our *a priori* predictions.

[9]For transparency, we also report the full findings from this omnibus test here. We find main effects of (a) Reaction, $F(1, 443) = 448.40$, $p < 0.001$, $\eta_p^2 = 0.503$, such that people expected targets would feel greater anger ($M = 89.14$, $SE = 0.82$) than they would display ($M = 62.07$, $SE = 1.36$), and (b) Attribute, $F(1, 443) = 9.92$, $p = 0.002$, $\eta_p^2 = 0.022$, such that people expected targets described in terms of physical strength would feel/display greater anger ($M = 78.52$, $SE = 1.29$) than targets described in terms of physical attractiveness ($M = 62.07$, $SE = 1.36$). These were qualified by interactions of Reaction and Attribute Level, $F(1, 443) = 5.95$, $p = 0.015$, $\eta_p^2 = 0.013$, of Reaction, Target sex/gender and Attribute, $F(1, 443) = 4.02$, $p = 0.046$, $\eta_p^2 = 0.009$, as well as the four-way interaction reported above.

Do people infer that stronger men and more physically attractive women will display greater anger? Yes. As predicted, we find that people (a) expect physically stronger (versus weaker) men to *enact* significantly greater anger at the man thwarting them, $F(1,443) = 4.55$, $p = 0.033$, $\eta_p^2 = 0.010$, 95% CI = (0.91, 22.08) and (b) also expect more (versus less) physically attractive women to *enact* significantly greater anger at the woman thwarting them, $F(1,443) = 8.21$, $p = 0.004$, $\eta_p^2 = 0.018$, 95% CI = (5.03, 27.00). See **Figure 1A**, and see **Table 1** for means (SEs).

People did not expect these same patterns for feelings of anger (ps > 0.650). Additionally, there were no significant differences in expected acts or feelings of anger as a function of men's varying physical attractiveness (*p*s > 0.060) or women's varying physical strength (*p*s > 0.685).

We also explored other, not-predicted possible differences.

Comparing target attributes (strength versus attractiveness), people expect physically stronger (versus more attractive) men to enact significantly greater anger toward thwarters, $F(1,443) = 7.94$, $p = 0.005$, $\eta_p^2 = 0.018$, 95% CI = (4.70, 26.35), and also to feel significantly greater anger toward thwarters, $F(1,443) = 4.52$, $p = 0.034$, $\eta_p^2 = 0.010$, 95% CI = (0.53, 13.58). There were no significant differences for men low in strength versus men low in attractiveness (*p*s ≥ 0.068). People also expected physically weaker (versus less attractive) women to enact significantly greater anger, $F(1,443) = 10.17$, $p = 0.002$, $\eta_p^2 = 0.022$, 95% CI = (6.62, 27.89). There were no significant differences for women high in strength versus women high in attractiveness (*p*s ≥ 0.540).

Comparing target sex/gender, we find that people expected more physically attractive men (versus women) to enact significantly more anger toward thwarters, $F(1,443) = 5.70$, $p = 0.017$, $\eta_p^2 = 0.022$, 95% CI = (1.43, 14.79). People also reported expecting less attractive men (versus women) to enact greater anger, $F(1,443) = 10.00$, $p = 0.002$, $\eta_p^2 = 0.022$, 95% CI = (6.42, 27.51). No other significant target sex/gender differences emerged (*p*s > 0.300).

In every case, targets were also expected to feel more anger than they were expected to display (*p*s < 0.001).

TABLE 1 | Means (*SE*s) of expected levels of anger display from different targets.

	Male target		Female target	
	High	Low	High	Low
Physical strength				
Feel	89.59(2.33)	92.83(2.27)	91.07(2.31)	91.35(2.29)
Act	70.69(3.86)	59.20(3.75)	67.80(3.83)	65.63(3.79)
Physical attractiveness				
Feel	82.54(2.37)	87.00(2.25)	90.65(2.44)	88.11(2.33)
Act	55.17(3.93)	65.34(3.73)	64.39(4.04)	48.38(3.86)

Experiment 2

In the sample from India, we again conducted the same 2 (Reaction: Feelings, Actions) x 2 (Target sex/gender) x 2 (Attribute) × 2 (Level: High/Low) mixed-factors ANOVA to explore people's expectations of targets' angry feelings and actions in response to being thwarted. In light of a (barely) significant four-way interaction, $F(1, 370) = 3.88$, $p = 0.050$, $\eta_p^2 = 0.010$, we examined our *a priori* predictions.[10]

[10]For transparency, we also report the full findings from this omnibus test. We find main effects of (a) Reaction, $F(1, 370) = 45.69$, $p < 0.001$, $\eta_p^2 = 0.110$, such that people expected targets would feel greater anger ($M = 70.16$, $SE = 1.17$) than they would display ($M = 60.98$, $SE = 1.34$), and (b) Target sex/gender, $F(1, 370) = 3.92$, $p = 0.048$, $\eta_p^2 = 0.010$, such that people expected male targets would feel/display greater anger ($M = 67.66$, $SE = 1.50$) than female targets ($M = 63.48$, $SE = 1.48$). These were qualified by interactions of Reaction and Attribute level, $F(1, 370) = 6.43$, $p = 0.012$, $\eta_p^2 = 0.017$, and Reactions, Target sex/gender and Attribute, $F(1, 370) = 8.24$, $p = 0.004$, $\eta_p^2 = 0.022$, as well as the four-way interaction reported above.

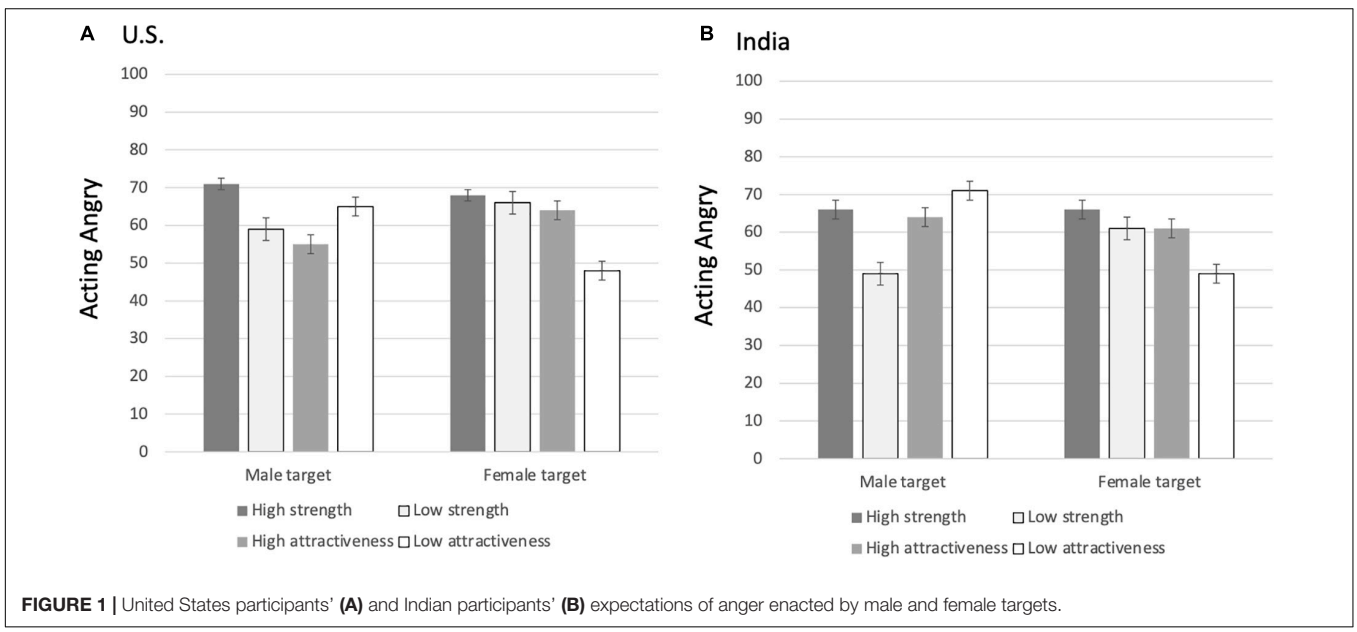

FIGURE 1 | United States participants' **(A)** and Indian participants' **(B)** expectations of anger enacted by male and female targets.

Do people infer that stronger men and more physically attractive women will display greater anger? Yes. Replicating the pattern of findings from Experiment 1's United States sample, we again find that people (a) expect physically stronger (versus weaker) men to *enact* significantly greater anger, $F(1, 370) = 9.49$, $p = 0.002$, $\eta_p^2 = 0.025$, 95% CI = (6.08, 27.53) and (b) also expect more (versus less) physically attractive females to enact significantly greater anger, $F(1, 370) = 4.59$, $p = 0.033$, $\eta_p^2 = 0.012$, 95% CI = (0.95, 22.29). See **Table 2** for means (*SE*s) and see **Figure 1B** (above).

People did not expect these same patterns for feelings of anger (ps > 0.650). Additionally, there were no significant differences in expected enactment or feelings of anger as a function of men's physical attractiveness (*p*s > 0.200) or women's physical strength (*p*s > 0.300).

We also explored other, not-predicted possible differences.

Comparing target attributes (strength versus attractiveness), we find that people expect less attractive men to enact more anger than weaker men, $F(1,370) = 16.30$, $p < 0.001$, $\eta_p^2 = 0.042$, 95% CI = (10.50, 32.34). People also expected weaker women to enact significantly greater anger than less attractive women, $F(1,370) = 4.97$, $p = 0.026$, $\eta_p^2 = 0.013$, 95% CI = (1.41, 22.48). There were no other significant differences comparisons here (*p*s ≥ 0.300).

Comparing target sex/gender, people expected weaker men (versus women) to enact significantly less anger toward thwarters, $F(1, 370) = 5.70$, $p = 0.017$, $\eta_p^2 = 0.015$, 95% CI = (2.22, 22.88). People also expected less attractive men (versus women) to feel marginally more anger, $F(1, 370) = 3.711$, $p = 0.055$, $\eta_p^2 = 0.010$, 95% CI = (0.20, 18.95), and to enact significantly more anger, $F(1, 370) = 14.87$, $p < 0.001$, $\eta_p^2 = 0.039$, 95% CI = (10.50, 32.34). No other significant target sex/gender differences emerged (*p*s > 0.200).

Unlike in the United States data, people expected most—but not all—targets to feel significantly greater anger than they would display (*p*s < 0.050). The exceptions were for men low in physical attractiveness ($p = 0.301$), women high in physical strength ($p = 0.718$), and women high in physical attractiveness ($p = 0.091$).

DISCUSSION

What cues do people use to infer a stranger's status? The present data suggest that the cues people use to infer a target's status depends on the target's gender. Specifically, people use men's physical strength and women's physical attractiveness as cues of their high status.

Here, we predicted and found that social perceivers—both in the United States and in India—inferred that men who were physically stronger (versus weaker) and women who were more (versus less) physically attractive would enact more anger at same-sex/gender others who thwarted them (i.e., cut in front of them in a line). These expectations were nuanced and specific. People did not expect women's physical strength or men's physical attractiveness to significantly influence anger displays. People also did not expect such differences in people's *feelings* of anger at being thwarted. Again, this pattern of results implies that, at least across these two nations, physical strength and physical attractiveness render men and women, respectively, higher status in the eyes of social perceivers.

These findings are consistent with literature suggesting that physical formidability is a cue of male status, and they also add to the growing body of work suggesting that physical attractiveness is a cue of female status (e.g., Sell et al., 2009; Buss et al., 2020). These findings also provide some support for the utility of the emotion expectation paradigm used here. This paradigm might be an effective tool for examining (other) cues of status in third-party perception, and thus helping to answer the broad, understudied question of how status, which exists in the eyes of others, is perceived and allocated. Indeed, myriad possible status features can be inserted into this paradigm—as in vignettes describing men and women with great riches (versus poverty), great notoriety (versus none), and so on—to test which other cues are used to infer people's status.

TABLE 2 | Means (*SE*s) of expected levels of anger display from different targets.

	Male Target		Female Target	
	High	Low	High	Low
Physical strength				
Feel	73.33(3.34)	71.18(3.42)	67.50(3.34)	69.48(3.09)
Act	65.65(3.81)	48.85(3.90)	66.10(3.81)	61.40(3.52)
Physical attractiveness				
Feel	72.06(3.31)	74.89(3.34)	67.31(3.17)	65.51(3.54)
Act	64.44(3.66)	70.87(3.81)	61.07(3.62)	49.45(4.04)

IMPLICATIONS FOR MALE AND FEMALE STATUS

We focused here on straightforward predictions about features highly likely to be linked to estimations of men's and women's status. The link between men's physical strength and inferences of their higher status may be especially unsurprising, as larger and stronger males are known to receive and effectively command priority access to contested resources (e.g., De Waal and Waal, 2007; Cheng et al., 2013; Franz et al., 2015; Durkee et al., 2018, 2020). However, this finding may also underscore the evolved nature of the status features that the mind is attuned to. Physical strength may have been highly predictive of an animal's success in ancestral environments but is less reliably predictive of people's success in modern settings (e.g., universities, workplaces). Nevertheless, in line with other work (Buss et al., 2020), the present findings suggest that social perceivers still use men's physical strength as a status cue.

As we argued above, default conceptualizations of status may often privilege historically male-typical instantiations of status (e.g., success in physical conflicts) and concomitant cues (see also Benenson, 1999; Lukaszewski et al., 2016; von Rueden et al., 2018; Garfield et al., 2019; Hagen and Garfield, 2019). These cues may or may not lead people to deem the women possessing them as high status. Thus, we examined whether women were inferred

to have higher status as a function of their physical strength but also of their physical attractiveness (see Sell et al., 2009; Buss et al., 2020). Indeed, robust evidence suggests that more attractive women have more, easier access to contested resources (e.g., help from strangers, money, social support, attention; Benson et al., 1976; Mulford et al., 1998; Solnick and Schweitzer, 1999; Rosenblat, 2008; Rosen and Underwood, 2010; Parrett, 2015; Bhogal et al., 2016; Eisenbruch and Roney, 2020).

Yet whereas much related work focuses on attractiveness as a cue of female fertility, and thus women's ability to confer (or withhold) reproductive benefits, the benefits of female beauty need not be so limited. First, what connotes female beauty will vary across cultures and eras. As such, not all aspects of physical attractiveness are necessarily going to be linked to fertility.

Second, more physically attractive people might also be preferred as social partners for a range of reasons over and above those linked to furthering one's own reproductive access or that of one's kin (e.g., Eisenbruch and Roney, 2020). Third, female beauty might also reliably covary with other features that enhance women's ability to inflict costs on or generate benefits for others. For example, some work suggests that girls' earlier life physical attractiveness can be leveraged into popularity and other possible forms of status that provide priority access to contested resources (Elder, 1969; Krendl et al., 2011; Lee et al., 2018; Vaillancourt and Krems, 2018). Such attractiveness might garner women "notoriety or prominence within the cultural consciousness," aspects of social status that, in turn can improve women's abilities to produce high-quality offspring (Rucas, 2015, p. 117). Indeed, this link between female beauty and attainment of other status features may be exacerbated by modern technologies in the economy of human attention. Status features garner attention across a range of social species (e.g., Vaughn and Waters, 1981; LaFreniere and Charlesworth, 1983; McNelis and Boatright-Horowitz, 1998; Maner et al., 2008; Foulsham et al., 2010). Notably, modern technological applications (e.g., Instagram) might accelerate the translation of human attention—which can be captured *via* displaying status cues (e.g., female beauty, great riches)—into social influence, income, and other facets of status.

This implies a possible reframing for some explanations of women's appearance enhancement, whereby motivations and tendencies to enhance appearance can and perhaps should be viewed as a competitive strategy to access more than (male) mates—i.e., to compete for status (Blake and Brooks, 2019; Davis and Arnocky, 2020; Eisenbruch and Roney, 2020; Fisher and Krems, in press; Bradshaw and DelPriore, 2021; see text footnote 5). For example, Blake and Brooks (2019) found that women's intended self-sexualization (i.e., wearing revealing clothing) is partly driven by status-related goals. To the extent that beauty can garner status, and such status can benefit women (by, e.g., conferring preferential access to survival- and reproduction-limiting resources), then perhaps we should expect women to compete for status (and not only mates) *via* appearance enhancement (and/or the derogation of rivals' beauty).

We also suggest that there are many possible cues/features of female status that remain unexplored. To identify these, at one level of abstraction, one might start by asking in which ways girls and women generate benefits for others (Durkee et al., 2020)—such as by being apt (allo)mothers, friends, and advisors, desirable romantic partners, and so on—and then ask which cues might reflect those aptitudes. A similar way to attack this problem might be to examine females' ability to generate those benefits perhaps historically more often associated with males, such as political leadership (e.g., Price and van Vugt, 2014; von Rueden et al., 2014). Might there be features that contribute more strongly to perceptions of a woman's leadership ability, and are cues of these glossed as status cues?

We might similarly ask what features render a woman better able to inflict costs on people. For example, females prefer indirect tactics of aggression to direct ones (e.g., gossip over physical violence) (e.g., Campbell, 1999; Vaillancourt, 2013; Benenson, 2014). Perhaps greater popularity or network centrality, for example, could help derogatory gossip spread more effectively (e.g., Hess and Hagen, 2006, 2019), making popular and/or network-central women more formidable among other women. If so, cues of these could be used to infer female status.

An additional, related tack generates still more overlooked status cues *via* acknowledging females' use of social partners as tools for inflicting costs on others (i.e., in enacting social or relational aggression; Campbell, 1999; Hess and Hagen, 2006, 2019; Vaillancourt, 2013; Benenson, 2014). Consider a woman who can successfully inflict costs on others by inciting her male kin to physically harm those others, or a woman who can withhold benefits from others by asking her high-value male partner or her group of female friends to refrain from allying with those others. Such indirect routes to status may have long been used by women—not unlike one child demanding better treatment from another because "my dad can beat up your dad," or one man receiving preferential treatment from another because the former is the son of someone important. Thus, it may be time to examine the possibility that perhaps women might especially (but certainly not exclusively) enjoy *indirect status*—and perhaps particularly from their associations with strong, rich, or otherwise powerful males. To be exceedingly clear, this does not discount females' ability to gain indirect status *via* other females or to gain direct status in their own rights. Rather, on this view, 'possession' of such associates—or of cues connoting the presence of such associates—might lead social perceivers to infer such female possessors as having high status. This might work similarly as for better-studied male targets, who can gain indirect status from coalitional partners, for one example (e.g., von Rueden et al., 2008, 2019).

One might also wonder why physically stronger (versus weaker) women or more (versus less) physically attractive men were not deemed higher status. As to why female strength did not influence third-party perceptions, it is possible that our sample sizes were insufficient to allow us to detect genuine but small effects (e.g., Sell et al., 2016). It is also possible that, as discussed above, women's increased physical size or strength would not have historically helped women in agonistic conflicts. Moreover, that weaker women were expected to display more anger than less attractive women might even suggest that greater physical strength is viewed as masculine and perhaps even undesirable in women; by the same token, weaker women might be deemed more feminine and attractive, and thus expected to display

greater anger. For men, there are several possibilities, including that male attractiveness is indeed a status cue, but the size of that effect was smaller than what we were able to detect (e.g., Sell et al., 2016). Alternatively, perhaps descriptions of physical attractiveness feminized targets in social perceivers' views, thus making those targets less high status in third-party perception (see Buss, 1990; Buss et al., 2020).

LIMITATIONS AND FUTURE DIRECTIONS

As noted above, we hardly exhausted the possible cues of status. Future work might use this same paradigm to explore third-party perception of other, additional features. Future work might also explore whether the same features that rendered people higher status here act similarly when thwarters are other-sex/gender. For example, on average, even a weaker man could inflict catastrophic physical damage on a stronger woman. Yet threatening or enacting such harm is now highly taboo in most societies. Would people still expect this man to display anger at a thwarting woman? Additionally, whereas we manipulated the strength and attractiveness of targets, we gave no information about *thwarter* strength or attractiveness. Our same logic would predict that third-party perceivers should expect less anger displayed when thwarters possess relatively greater status cues (e.g., greater physical strength). Moreover, it is possible that some status cues are more or less effective as a function of the target and thwarter sex/gender. For example, perhaps male (versus female) prospective thwarters would be deemed especially likely to defer to physically attractive female targets. Indeed, such expectations of deference may be another front for exploration in a similar paradigm as we used here.

Are these features—physical strength and physical attractiveness—really cues of *status* (rather than something else)? This is a fair question, especially given that there exist various conceptualizations of status (e.g., rank, reputational regard, power, dominance- and prestige-based status; Cheng et al., 2013, 2021; Galinsky et al., 2015; Buss et al., 2020; Durkee et al., 2020). Moreover, disagreements persist over the extent to which humans have dominance-based status, and thus the extent to which humans confer status upon conspecifics able to inflict costs on others, or instead emphasize status conferral upon those able to generate benefits (e.g., Cheng et al., 2021, Durkee et al., 2020; Chen Zeng et al., 2022). It is possible, for example, that male anger displays are linked primarily to dominance-based status, which would be consistent with the functions of anger expressions for expressors (essentially making expressors look more aggressively formidable). At the same time, other work suggests that male physical strength is also associated with the ability to generate benefits (Lukaszewski et al., 2016; Durkee et al., 2020), suggesting that this cue might also be linked to other forms of status associated with prestige and reputation (see, e.g., Buss et al., 2020). This same question should be asked with respect to women: Is physical attractiveness primarily related to dominance-based status? It might not seem so at first, but to the extent that more physically attractive women are able inflict greater costs on rivals (Fisher and Cox, 2009) or are able to translate their appearance into other forms of status (e.g., popularity) that, in turn, are linked to the perpetration of hierarchy-maintaining aggression (see Vaillancourt and Krems, 2018), it is certainly possible.

Moreover, this is a fair question given that we have not directly measured status perception. We are explicit in our logic that greater inferences of target anger display should track—and would, in fact, seem to track—cues associated with status in third-party perception. We underscore the soundness of this logic, but also acknowledge that our paradigm is not as straightforward as asking whether participants deem stronger versus weaker targets high status. Such a face-valid method might be an apt, complementary means for assessing which features render targets high status in social perception. A broader multi-method approach might also use non-survey social, cognitive, and behavioral methods. For example, higher status individuals capture greater attention (e.g., Chance, 1967; Vaughn and Waters, 1981; LaFreniere and Charlesworth, 1983; McNelis and Boatright-Horowitz, 1998; Maner et al., 2008; Foulsham et al., 2010). Thus, examining attentional adhesion to targets varying in strength or attractiveness could allow for inferences of whether these features render targets high status in third-party perception.

We tested and found support for predictions in two cultures. Future work would ideally examine these and additional status features across a range of cultures, including small-scale societies. One issue to anticipate in doing so is that there can be different norms for emotion display (including anger; Park et al., 2013; see also Rychlowska et al., 2015). All else equal with respect to emotion display norms, a fruitful area of cross-cultural examination might be in identifying specific features linked to status in various cultures and examining them within and across cultures using this paradigm (see, e.g., Sznycer et al., 2016).

Finally, we point out the possibility that some people might not readily deem female physical attractiveness a cue of *genuine* status—at least not as readily as they might otherwise deem male physical strength, wealth, leadership positions, and the like. Women themselves acknowledge beauty as bringing power, at least over men; for example, in 2020 the novel by Chelsea G. Summers, the female protagonist thinks, "...I wanted these men to lust for me because...I knew that lust was power." Yet we also acknowledge that some people might be offended that female beauty "counts" as a status cue in third-party perception, including for well-meaning reasons related to gender equality. It is an empirical question as to whether this form of status is truly given short shrift in people's social judgments—or if honoring female attractiveness as a cue of status in any way disadvantages women, as some might expect it to. But ultimately, this meta-question of the impact of people's association between female physical attractiveness and status is distinct from the findings here, which suggest that people in the United States and India use both men's physical

strength and women's physical attractiveness as cues of those targets' high status.

CONCLUSION

People face an adaptive challenge in inferring other people's status levels. This raises an important but relatively understudied question about what cues people use to make these status inferences. Here, we leverage robust associations between anger and status—that social perceivers expect higher-status people to display more anger (Tiedens et al., 2000; Tiedens, 2001; Hess et al., 2005; Hareli et al., 2009; Sell et al., 2009, 2017)—to explore what some of those status-cueing features might be. In line with past work (e.g., Buss et al., 2020), we also examined whether the features that cue men's high status might be distinct from those that cue women's high status. We find that United States and Indian social perceivers expect men with more (versus less) physical strength and women with more (versus less) physical attractiveness to display greater anger when thwarted by another person. This pattern of anger expectations implies that United States and Indian social perceivers use men's physical strength and women's physical attractiveness as cues to those targets' high status.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Oklahoma State IRB. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

JK developed hypotheses with critical feedback from LM, DS, JB-C. LM, VS, KD, and NR drafted materials with critical feedback from JK and DS. JK, LM, and VS worked on data analysis. JK drafted the manuscript with critical feedback from DS, JF, NR, and JB-C. All authors contributed to the article and approved the submitted version.

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APPENDIX A: VIGNETTE EXAMPLES

Target descriptions

Alex is taller than most other men (women). In fact, Alex often towers over them. Alex is also much stronger than most men (women); even from far away, Alex looks very muscular and imposing compared to most other men (women).

Alex is shorter than most men (women). In fact, other men (women) often tower over Alex. Alex is also much smaller than most men (women); even from far away, Alex looks much slighter compared to most other men (women).

Alex is a very attractive man (woman). People definitely take notice of Alex when he (she) walks into a room because he (she) is so good-looking compared to most other men (women).

Alex is a very unattractive man (woman). People rarely take notice of Alex when he (she) walks into a room because he (she) is so unattractive compared to most other men (women).

Action

Today, Alex is on his (her) way home. He (She) spent the entire day doing annoying and tedious paperwork at the office. His (Her) phone died, so he couldn't listen to music. He (She) also forgot his lunch, so on his way home, Alex stops in to grab something quick to eat near his (her) bus stop. Busses run every hour, so he (she) should make the next bus as long as he (she) is quick. He (She) can't wait to get home!

Right then, another man (woman) *deliberately* cuts in line in front of Alex, and places a big, complicated order. Now Alex will miss the bus, meaning spending another hour in this dirty, boring part of the city.

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Gender Differences in the Perceived Behavior of Narcissistic Leaders

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Although narcissists often emerge as leaders, the relationship between leader narcissism and follower performance is ambiguous and often even found to be negative. For women, narcissism seems especially likely to lead to negative evaluations. Since narcissists have the tendency to be impulsive and change their minds on a whim, they may come across as inconsistent. We propose "inconsistent leader behavior" as a new mechanism in the relationship between leader narcissism and follower performance and argue that leader gender plays an important role in whether narcissistic leaders are perceived as inconsistent. Specifically, we expect leader narcissism to have a negative relationship with follower performance through perceived inconsistent leader behavior, especially for female leaders. Thus, we examine leader gender as a personal factor moderating the relationship between narcissism and perceived inconsistent behavior. Also, as perceived inconsistency is likely less problematic when a good relationship exists, we examine leader–member exchange (LMX) as a contextual condition moderating the relationship between leader behavior and follower performance. We test our moderated mediation model in a multi-source study with 165 unique leader–follower dyads. As expected, leader narcissism was positively related to perceived inconsistent leader behavior, and this relationship was stronger for female leaders. Inconsistent leader behavior was negatively related to follower performance, but only when LMX was low. Our research highlights that perceived behavioral inconsistency can be problematic and—for female leaders—provides an explanation of the negative relation of leader narcissism with follower performance and of the inconsistencies in evaluations of narcissistic leaders' effectiveness.

Keywords: leader narcissism, gender, inconsistent leader behavior, LMX, follower task performance

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INTRODUCTION

Narcissism has attracted attention in leadership research for over 20 years. In line with the higher leadership ratings narcissists often receive, they tend to emerge as leaders (Brunell et al., 2008; Nevicka et al., 2011a) and are relatively overrepresented in organizations (Grijalva et al., 2015). However, once narcissists occupy a leadership position, overall they do not seem to be more effective than their less-narcissistic counterparts (Grijalva et al., 2015) and despite initially making a leaderlike impression, over time they are often regarded negatively (Lubit,

2002). This may be due to the characteristics inherent in narcissism.

Narcissistic characteristics overlap with typical agentic traits, such as arrogance (Campbell et al., 2002), exploitativeness, egocentrism (Sedikides and Campbell, 2017), opportunism (Konrath et al., 2016), and impulsivity (Vazire and Funder, 2006; Malesza and Ostaszewski, 2016). These characteristics of narcissism imply an element of irrationality and unpredictability, suggesting that narcissistic leaders are more likely to be perceived as displaying inconsistent leader behavior. Inconsistent leader behavior is behavior that is perceived by followers as varying across situations in erratic and seemingly random ways. These leader behaviors are difficult to predict as they often appear to not fit the situation or differ from previous behavior in a similar situation.

Research has shown that gender impacts the evaluation of characteristics and behaviors, such that men are perceived differently than women depending on the socially expected and accepted sex role behavior (Rudman and Phelan, 2008). Several of the characteristics of narcissists do not fit with the characteristics typically associated with women. For instance, narcissists' dominant and self-promoting (agentic) behavior is likely to clash with the communal female gender stereotype (e.g., Rudman, 1998). Though this clash can lead to an increase in perceived competence, at the same time it likely leads to a decrease in likeability which is called the backlash effect (Rudman, 1998). The backlash effect explains negative outcomes of incongruency with gender stereotypes, especially for women. In line with literature on the backlash effect, women have been found to be penalized for displaying dominance (Grijalva et al., 2015). For example, agentic behavior by women is positively related to hiring discrimination (Rudman and Glick, 2001; Phelan and Rudman, 2010) and negatively impacts voting preferences, whereas no such relationship exists for men (Okimoto and Brescoll, 2010). Furthermore, people assign less status and lower salaries to women expressing anger as compared to men expressing anger (Brescoll and Uhlmann, 2008). Specifically for a leadership context, gender has been found to impact the relationship between leader narcissism and perceived leader effectiveness where female narcissistic leaders are rated as less effective than male narcissistic leaders (De Hoogh et al., 2015). Previous research has also demonstrated that perceivers encode leader behavior in relation to leader gender (Scott and Brown, 2006; Sczesny et al., 2006). However, to our knowledge, the mechanisms underlying gender differences in the evaluation of narcissistic leaders are not yet clear. Here, we propose that inconsistent leader behavior forms a mechanism through which leader narcissism is negatively related to outcomes and that this will be exacerbated for female leaders.

Inconsistent behavior reflects behavior that typically relates to impulsivity and opportunism which are agentic traits (as they both reflect power and selfishness as typical features of agency) that are linked to narcissism (e.g., Jonason and Fletcher, 2018). Impulsivity is characterized by being rash and unpredictable (e.g., Dickman, 1990; Bari and Robbins, 2013). Opportunism is related to efforts to gain an advantage from a situation, often at the expense of others (Wong et al., 2005). Considering that men are expected to display dominant and agentic behavior (Eagly et al., 1981) and are stereotypically thought to be high on impulsiveness (Löckenhoff et al., 2014), displaying inconsistent behavior is congruent with the masculine stereotype. When men display agentic and inconsistent behavior, this may thus be interpreted as a display of power rather than erratic behavior.

Women, on the other hand, are expected to act according to rules and norms and to not display divergent behavior, such as agentic behavior (Eagly et al., 1981). Drawing on Sherif and Hovland's (1961) classic judgment model we propose that the negative aspects of narcissism in terms of being divergent and unpredictable are discrepant from people's stereotypes about women and thus more salient when evaluating the behavior of female narcissistic leaders. For women, showing agentic inconsistent behavior may come across as erratic and negatively stands out. This behavior for females is highly visible, whereas for male leaders being unpredictable and impulsive is congruent with the expected (agentic) sex role behavior and will stand out less. We thus expect that the effects of narcissism on the perception of inconsistent leader behavior are contingent on leader gender.

The perception of inconsistent leader behavior in turn negatively affects follower performance as it acts as a stressor that is likely to deplete followers' energetic resources (Burger and Arkin, 1980). Previous research suggests that followers' response to leader behavior is influenced by the quality of the leader–follower relationship, often referred to as leader–member exchange (LMX). According to LMX theory, leaders do not treat every subordinate the same, different types of relationships develop between leaders and followers, and the quality of these relationships can range from low to high (e.g., Liden et al., 1997). Followers in a high-quality relationship have higher trust in their leader and are more committed to the leader. This makes them more open to social (leader) influence and implies they respond more favorably to their leader's behaviors than followers in a low-quality relationship (Piccolo and Colquitt, 2006; Michel and Tews, 2016). In line with this, we argue that the effects of perceived inconsistent leader behavior on follower performance are dependent on the quality of the relationship between leader and follower. For followers in a high-quality LMX, where best intent of the leader is assumed and trust in the leader is high, the negative effects of perceptions of inconsistent leader behavior on followers will be reduced compared to a low-quality LMX relationship. We thus test a (first-stage and second-stage) moderated mediation model that may help to clarify the link between leader narcissism and follower performance and the effect of gender on this relationship (see **Figure 1**).

With this paper, we aim to contribute to several literatures. First, we add to the research on gender differences by investigating the effect of gender on the perception of narcissistic leader behavior. In doing so we contribute to the understanding of why narcissism and related behaviors are differentially perceived for men and women. Second, explanatory variables for the negative impact of narcissism on follower performance have rarely received attention to date (for an exception, see Nevicka et al., 2011b). Here, we introduce the concept of inconsistent behavior to the literature on narcissism and identify it as a mechanism through which leader narcissism may relate to

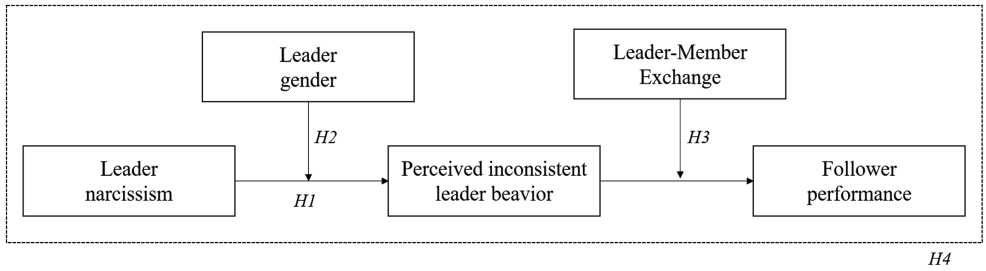

FIGURE 1 | Proposed moderated mediation model.

follower performance. Third, we answer a call of leadership scholars who have emphasized the need for theory development on behavioral inconsistency (e.g., Simons, 2002), which has only recently started to receive (limited) research attention (e.g., Dineen et al., 2006; Zhang et al., 2015). Finally, we propose LMX as a contingency variable to mitigate the negative effects of perceived inconsistent leader behavior on follower performance hereby adding to the literature showing the moderating effects of LMX on followers' reactions to their leaders' behavior.

Leader Narcissism

Narcissism describes a personality trait that involves a lack of empathy, inflated self-esteem, and a need for admiration (Miller and Campbell, 2008). The lack of empathy that characterizes narcissists implies a disrespect and disregard of others (Konrath et al., 2016) and over time this often creates difficulties in maintaining close relationships (Campbell and Foster, 2002). Their inflated self-esteem biases narcissists' self-perceptions by making them dream about personal success, glory, and power, and by stimulating them to see themselves as superior to others (Paulhus and Williams, 2002; Rosenthal and Pittinsky, 2006). Narcissists have high levels of confidence and optimism and seek power and authority over others (Raskin and Terry, 1988; John and Robins, 1994). Narcissists also view themselves as very intelligent, special, and unique and have a tendency to be arrogant (Raskin and Terry, 1988; Campbell et al., 2002; Judge et al., 2006). Narcissists' self-view, however positive, is unstable (Baumeister et al., 2000). They need admiration and constant reaffirmation of their self-implied superiority (Rosenthal and Pittinsky, 2006), which is why they engage in social displays of ability, act in ways to reinforce their superiority, and favor bold actions that attract attention (Chatterjee and Hambrick, 2007; Smith and Webster, 2018).

Research shows that people scoring high on narcissism score low on ethics (Brown et al., 2010). Narcissism forms a predictor of counterproductive work behavior (Grijalva and Newman, 2015) and lying (Giammarco et al., 2013). Narcissists are erratic and often act impulsively (Jones and Paulhus, 2011), and they are unable to learn from mistakes (Campbell et al., 2004) or to react to negative feedback in an appropriate way (Barry et al., 2006). In what follows, we focus on a so far under-researched aspect of narcissism and propose that the impulsivity of narcissists can lead to narcissistic leaders being perceived as displaying inconsistent leader behavior, especially for female leaders, which might explain the negative relationship between leader narcissism and follower performance.

Narcissism and Gender

Research has shown that the same characteristics are evaluated differently when displayed by men and women, depending on social expectations and accepted role behavior (Rudman and Phelan, 2008). Social role theory suggests that women are expected to be communal (helping, understanding) while men are expected to be agentic (dominant, arrogant; Eagly, 1987). These gender-related expectations are also found for leaders. Previous research has demonstrated that perceivers encode leader behavior in relation to leader gender (Scott and Brown, 2006; Sczesny et al., 2006). For example, women are more likely to be expected to have a servant leadership style, whereas men are more likely to be expected to have an authoritarian style (Hogue, 2016).

Many narcissistic characteristics overlap with agentic traits (Campbell et al., 2002), which implies that narcissism is more in line with stereotypical masculine traits as compared to feminine traits. The dominant and self-promoting behavior that is typical for narcissists, does not match the communal leadership style that is expected of female leaders (e.g., Rudman, 1998). Yet, being incongruent with one's gender role might lead to negative evaluations, resulting in a backlash effect for agentic female leaders (e.g., Rudman, 1998; Eagly et al., 2000). Indeed, narcissistic leaders are evaluated negatively when they are women, but not when they are men (e.g., De Hoogh et al., 2015). Here, we build on this work on narcissism and gender. Based on the judgment model of Sherif and Hovland (1961) we argue that behavior that is incongruent with one's stereotype is more salient because of the contrast between the behavior displayed and the behavior expected based on gender role expectations and is therefore perceived more negatively. While prior research has focused particularly on the dominance and assertiveness of narcissistic leaders (Rosenthal and Pittinsky, 2006), other narcissistic characteristics have received less attention. Here, we explore narcissists' unpredictability and inconsistency as under-researched characteristics.

Inconsistent Leader Behavior

Previous work in the field of leadership has often described leadership styles as stable and constant, suggesting that leaders typically display one type of behavior (Hannah et al., 2014).

Even though early research based on contingency theory (e.g., Fiedler, 1967) already pointed out that leader behavior may differ from situation to situation (Utecht and Heier, 1976), only recently have researchers started to investigate the effects of leaders displaying multiple types of leader behavior (e.g., Johnson et al., 2012; Lanaj et al., 2016).

Most theories that address multiple leader behaviors, like contingency theory, leader versatility, and flexible leadership (Fiedler, 1967; Kaplan and Kaiser, 2003; Yukl and Mahsud, 2010), focus on leader's display of varying behavior in order to adapt to specific situational or personal demands. Here, we argue that leaders may also engage in varying behavior that is not *per se* perceived to be adjusted to a specific situation. For example, leaders might be approachable one moment and not the next without a clear reason. Differences or changes in leader behaviors that occur at different moments or in different spaces may have their roots in other contexts (e.g., meetings with top management that followers have no notion of may cause a change in actions), personality traits of the leader (e.g., impulsivity, instability), strategic intent (e.g., self-centered), or (lack of) competency. As followers lack knowledge of the source of the unpredictability, followers may perceive such variation in leader behavior as unpredictable, erratic, and inconsistent, and this may negatively impact followers and organizations, for instance, by undermining trust in the leader, distracting followers, and causing them stress.

So far, only few researchers have looked into such potentially negative behavioral variability. For example, Dineen et al. (2006) studied the effect of leader's inconsistency between words and actions on follower organizational citizenship behavior. Organizational citizenship behavior (OCB) can be defined as behavior that is not part of an employee's formal tasks, such as voluntarily providing assistance to colleagues or promoting the organization (e.g., Smith et al., 1983; Organ, 1988) or as "performance that supports the social and psychological environment in which task performance takes place" (Organ, 1988, p. 95). OCB is an important construct in organizational research as it is related to measures of organizational effectiveness (Podsakoff et al., 2009). In two separate field samples, Dineen et al. (2006) found that leader's consistency between words and actions is positively related to follower OCB. This suggests word-deed misalignment ("not walking your talk") may have negative consequences, especially considering the positive effects of OCB on organizational effectiveness. Also, another study suggested that when leaders who display ethical leader behavior are also seen to display passive leader behavior, this reduces the positive effects of the ethical behavior. Specifically, the findings show that passive behavior weakens the negative effect of ethical leader behavior on follower burnout (Vullinghs et al., 2020), again suggesting that varying leader behavior may have adverse consequences.

In this paper, we argue for an overarching type of inconsistent leader behavior, which is not limited to inconsistency between values and behavior or varying between different leadership styles. Leaders that display inconsistent leader behavior show different behavior in similar situations (e.g., stressing the importance of a specific goal 1 day, whereas the next day another goal is emphasized as most important) or treat similar followers differently (e.g., showing appreciation for the achievement of one follower, but not for similar achievements of another), which makes their behavior hard to predict for followers. Given that leaders have considerable power over organizational processes and outcomes, inconsistent leader behavior may be particularly impactful. Not being able to predict the behavior of their leader is likely to be cognitively and emotionally taxing for followers and thus may deplete resources and distract followers from their core tasks as they constantly feel the need to monitor their leader to make sense of the inconsistent behavior and understand the leader's intentions.

Narcissists are often described as opportunistic (Wink, 1991; Konrath et al., 2016) and impulsive (Vazire and Funder, 2006). On average, they score low on both empathy (Ames and Kammrath, 2004) and agreeableness (Paulhus, 2001). Narcissists are also characterized by an extreme impulsivity and *ad hoc* emotional reactivity and display more day-to-day variability and extremity in their emotions than less-narcissistic individuals (Emmons, 1987; Rhodewalt et al., 1998). Moreover, narcissists use other people to further their own goals (Campbell et al., 2005; Rosenthal and Pittinsky, 2006; Sedikides and Campbell, 2017; Den Hartog et al., 2020). They believe they deserve more than others and have a high sense of entitlement (Campbell et al., 2004). People with a sense of entitlement may see their own motivation as sufficient to act, thereby disregarding others' ideas, needs, and objections. They focus on acting on their desires, including ones that others might find rather questionable (Hofmann et al., 2012). This suggests that narcissists will easily alternate between behaviors depending on what they feel is best for them, or on a whim based on what they feel like in the moment. We propose this may lead to them being perceived by others as inconsistent.

Indeed, research has found narcissists to take advantage of specific situations. They are, for instance, more likely to engage in prosocial behavior when this behavior is highly visible than when no one can see it (Konrath et al., 2016). Moreover, narcissism is positively linked to impulsivity (Casillas and Clark, 2002), independent behavior, and lower ability to delay gratification (Vazire and Funder, 2006). Narcissists experience less conflict when acting on their desires (Hofmann et al., 2012). Moreover, research suggests that narcissists may strategically act in ways that imply they do not inhibit their urges and may intentionally engage in inconsistent, volatile behavior to convey a sense of power (Hart et al., 2017). Indeed, research shows that unpredictability may increase the (perceived) power of leaders (e.g., Sullivan et al., 2010; Van Kleef et al., 2011, 2012). We thus hypothesize:

Hypothesis 1: Leader narcissism is positively related to perceived inconsistent leader behavior.

Leader Gender and Perceived Inconsistent Behavior

As noted, the same traits and behavior can be evaluated differently for men and women. The Sherif and Hovland (1961) judgment model suggests that stereotype-inconsistent actions

are contrasted with gender role expectations. Behavior that is not expected is noticed more easily because of this contrast effect. For example, because women are expected to be more understanding and kind than men, a man is more likely to be noticed when comforting his child than a woman doing the same thing. Many studies found evidence for such stereotype-based contrast effects (e.g., Rudman and Phelan, 2010). We argue that such contrast effects with regard to gender stereotype may also affect perceptions of narcissistic leaders' inconsistent behavior.

Specifically, men are socialized to be more aggressive, autonomous, and bold, while women exhibit more conformity and self-discipline (Low, 1989). Also, research has consistently found gender differences in self-control with women exhibiting higher levels of self-control than men (LaGrange and Silverman, 1999). Whereas men generally score higher than women on self-reported emotional stability (Costa et al., 2001), evidence indicates an opposite pattern when it comes to stereotypes about this trait: men are on average stereotyped to be higher in impulsiveness than women (Löckenhoff et al., 2014). Drawing on Sherif and Hovland's (1961) stereotype-based judgment model we argue that perceivers expect less impulsive and unpredictable behavior from female leaders. Based on gender role expectations agentic, inconsistent actions stand out more for women than for men. These behaviors will thus be more salient when evaluating female narcissistic leaders than when evaluating male narcissistic leaders. Narcissists feel the power to do whatever they want, change their mind on a whim, and act on their impulses, which we hypothesize is more accepted, stands out less, and is less likely to be perceived as inconsistent for male leaders. In contrast for women, such impulsive behavior runs counter gender stereotypes and stands out compared to the expected agreeableness and thus such behavior is perceived as more inconsistent.

Hypothesis 2: Leader gender moderates the relationship between leader narcissism and perceived inconsistent leader behavior, such that female narcissistic leaders are perceived as displaying more inconsistent behavior than male narcissistic leaders.

Inconsistent Leader Behavior and Leader–Member Exchange

Inconsistent leader behavior pertains to showing varying behavior in similar situations, which makes it hard for followers to predict how an inconsistent leader will act. Prior research has suggested that inconsistent behavior may indeed play an important role in increasing experiences of unpredictability (O'Driscoll and Beehr, 1994; De Cremer, 2003). Predictability is valued very much by followers, and unpredictability is typically experienced as a strong stressor (e.g., Monat et al., 1972). For example, followers rate their leaders as more effective and more credible when they are able to predict their behavior (e.g., Johnson et al., 2012). Followers even prefer constant abuse over unpredictable abuse (Matta et al., 2017). A lack of perceived control over a situation and predictability are found to be related to motivational losses due to feelings of helplessness and related declines in performance (Burger and Arkin, 1980). In addition, unpredictable behavior of the leader is a stressor that is likely to deplete followers' resources and to distract their attention away from their core tasks. We therefore believe that perceived inconsistent leader behavior is negatively related to follower performance.

In previous research, LMX has been studied as an important factor influencing the effects of leader behaviors on followers (e.g., Schriesheim et al., 1998). According to Smircich and Morgan (1982), perceptions of and reactions to leadership are based on the interactions between leaders and followers. The quality of these interactions and the nature of the relationship between leader and follower determines the extent to which followers decide to resist the influence attempts of leaders or be open to them. In this sense LMX functions as "an anchor and context" (Lind, 2001, p. 73) for followers for interpreting and evaluating their leader's behavior. Indeed, findings suggest that the quality of the relationship between leaders and their followers defines the reaction of followers to leader behavior, where followers in a high-quality relationship have a more positive attitude toward their leader and assume their leader wants what is best for them. Followers in low-quality relationships, on the other side, have lower trust in their leader (Piccolo and Colquitt, 2006; Michel and Tews, 2016).

We study LMX as potentially having a buffering effect, where high levels of LMX might prevent a strong negative effect of perceived inconsistent leader behavior on follower performance. We argue that high-quality LMX makes followers more lenient toward their leaders (Michel and Tews, 2016), and we propose that perceived inconsistent leader behavior may then also have a less negative impact on follower performance under high-LMX leaders. For instance, followers might attribute perceived inconsistent leader behavior to the circumstances as they assume good leader intentions, or they may assume that there must be a good reason for the change in leader behavior that they might not know of. This logic also suggests that low-quality LMX might actually strengthen the negative relationship between perceived inconsistent leader behavior and follower performance as followers are likely more sensitive to and subsequently react more negatively to this type of behavior when feeling less connected to their leader. Thus, we expect:

> *Hypothesis 3*: LMX moderates the relationship between perceived inconsistent leader behavior and follower performance, such that the negative effect is weaker when LMX is high as compared to when LMX is low.

Overall, we expect that the indirect relationship between leader narcissism and follower performance *via* perceived inconsistent leader behavior is a function of leader gender (first-stage) and LMX (second-stage).

Hypothesis 4: Leader narcissism is related to follower performance *via* a conditional indirect effect, such that the negative indirect effect of leader narcissism on follower performance is strongest for female leaders with a low-quality relationship with their follower.

MATERIALS AND METHODS

Sample and Procedure

We tested our research model in a multi-source field study on a sample of 165 unique leader–follower dyads (i.e., 165 leaders and one follower for each leader, resulting in 165 followers) who worked in different organizations and across different industries. Our sample size is similar to that of samples used in previous studies looking at similar topics and models with the same amount of complexity (e.g., De Hoogh et al., 2015). Dyads were approached through contacts of students of a Dutch university and, if they agreed to participate, an email invitation to an online survey was sent. Confidentiality and the voluntary nature of participation were stressed in the accompanying message. To ensure anonymity, participants received a unique code to match the surveys. Participants could choose to complete the survey either in English or in Dutch. During data collection, reminders were sent to participants to increase the response rate. Most leaders were male (61.8%), the mean age was 41.98 years (SD = 11.62, 1 missing value). On average, leaders had worked for their current organization for 11.13 years (SD = 9.27, 9 missing values) and had worked with this specific follower for 3.86 years (SD = 4.63, 15 missing values). Most followers were female (50.3%), the mean age was 35.07 years (SD = 12.86). On average, followers had been working at their current organization for 7.98 years (SD = 9.23, 21 missing values).

Measures

Leaders rated their followers' performance and their own personality. Followers rated leader behavior and LMX. All variables were measured using a 7-point Likert-scale ranging from 1 (*strongly disagree*) to 7 (*strongly agree*).

Narcissism

Leaders filled in the 13-item version of the Narcissistic Personality Inventory (NPI-13; Gentile et al., 2013). Example items are: "I like having authority over others," and "I will usually show off if I get the chance." Coefficient alpha was 0.84.

Inconsistent Leader Behavior

As the concept of inconsistent leader behavior has received little attention in the leadership literature to date, we used a relatively new scale developed by Van Gerven et al. (2021) for measuring Inconsistent Leader Behavior (ILB). Four items were generated by Van Gerven et al. (2021) that matched the definition of inconsistent leader behavior and aimed to capture a one-dimensional focus on leader behavior that is perceived by followers as unpredictable and erratic and the authors provide validity information for this scale from multiple samples. Cronbach's alpha of this four-item scale was 0.87. For the full set of items see **Table 1**.

Leader–Member Exchange

Leader–member exchange was measured using the 8-item scale by Liden et al. (1993). Example items are: "My supervisor would be personally inclined to use his/her power to help me solve problems in my work," and "My supervisor understands my problems and needs." Coefficient alpha was 0.87.

Task Performance

Follower performance was measured using a five-item scale filled out by the leader (Williams and Anderson, 1991). Example items are: "My employee adequately completes assigned duties," and "My employee meets formal performance requirements of the job." Coefficient alpha was 0.87.

Control Variables

As the negative effects of narcissism might grow over time (Paulhus, 1998), we included tenure with the leader (in years) as control variable. We also checked whether survey language made a difference. Tenure did not significantly alter the variables or relationships in our study. Analysis conducted with language of the survey as a control also produced the same pattern of results. To conserve statistical power we therefore report the results without these control variables in what follows (e.g., Becker, 2005).

Measurement Model

A confirmatory factor analysis was conducted to determine whether the data conformed to the assumption that each of the proposed latent variables represents a separate construct. We randomly combined subsets of narcissism items to create three parcels of items. We did this only for the well-established and validated narcissism measure as this sufficiently reduced the sample size to parameter ratio, for the other variables we retained the single items and did not use parceling. Results for the measurement model indicated that the four-factor model fitted the data well, $\chi^2(164, 165) = 310.217$, $p < 0.01$, CFI = 0.915, TLI = 0.902, RMSEA = 0.074, SRMR = 0.059. Two alternative models, one in which the items of leader narcissism and inconsistent leader behavior were merged into one factor, $\chi^2(167, 165) = 532.806$, $p < 0.01$, CFI = 0.788, TLI = 0.759, RMSEA = 0.115, SRMR = 0.092, $\Delta\chi^2(3) = 222.589$, $p < 0.001$, one in which the items of inconsistent leader behavior and leader–member exchange were merged into one factor, $\chi^2(167, 165) = 541.421$, $p < 0.01$, CFI = 0.783, TLI = 0.753, RMSEA = 0.117, SRMR = 0.086, $\Delta\chi^2(3) = 231.204$, $p < 0.001$, exhibited significantly poorer fit. We also compared the four-factor model with a two-factor model with the items of leader narcissism and follower performance (both rated by the leader) in one factor, and inconsistent leader behavior and leader–member exchange (both rated by the follower) merged into the second factor. The four-factor model showed a significant better fit over the

TABLE 1 | Inconsistent Leader Behavior items.

Item number	Item
1	My supervisor behaves alternately.
2	My supervisor is inconsistent in his/her behavior.
3	My supervisor is hard to predict.
4	My supervisor behaves differently in comparable situations.

two-factor model, $\chi^2(169, 165) = 785.379$, $p < 0.01$, CFI = 0.643, TLI = 0.598, RMSEA = 0.149, SRMR = 0.125, $\Delta\chi^2(5) = 475.162$, $p < 0.001$.

RESULTS

Correlations

Table 2 presents the means, standard deviations, correlations, and reliabilities of the variables. Leader narcissism was positively correlated with perceptions of inconsistent leader behavior ($r = 0.21$, $p = 0.006$) and negatively with LMX ($r = -0.15$, $p = 0.049$). Perceptions of inconsistent leader behavior were negatively correlated with follower performance ($r = -0.16$, $p = 0.042$) and LMX ($r = -0.46$, $p < 0.001$). Finally, LMX was positively correlated with follower performance ($r = 0.22$, $p = 0.005$).

Hypothesis Testing

To test the hypotheses, we used the PROCESS macro (model 21, version 3.4, Hayes, 2013) in SPSS to conduct our analyses. All variables were mean centered prior to analyses (Aiken and West, 1991). The first step of this analysis examines the main effect of leader narcissism on inconsistent leader behavior. Hypothesis 1, leader narcissism is positively related to perceptions of inconsistent leader behavior, was supported. The results showed a significant main effect of leader trait narcissism on follower perceptions of inconsistent leader behavior ($B = 0.34$, SE = 0.12, $t = 2.91$, $p = 0.004$, 95% CI [0.11, 0.58]).

Next, we tested our full moderated mediation model. Hypothesis 2, leader gender moderates the relationship between leader narcissism and perceptions of inconsistent leader behavior, was supported ($B = 0.59$, SE = 0.24, $t = 2.41$, $p = 0.017$, 95% CI [0.11, 1.07]). Female narcissistic leaders were perceived to display more inconsistent behavior ($B = 0.71$, $SE = 0.20$, $t = 3.62$, $p < 0.001$, 95% CI [0.32, 1.09]), whereas narcissism was not related to perceptions of inconsistent behavior for male narcissistic leaders ($B = 0.12$, SE = 0.15, $t = 0.79$, $p = 0.428$, 95% CI [−0.17, 0.41]). The moderating effect of LMX on the relationship between perceptions of inconsistent leader behavior and follower performance (Hypothesis 3) was also supported ($B = 0.09$, SE = 0.04, $t = 2.11$, $p = 0.036$, 95% CI [0.01, 0.18]). Perceived inconsistent leader behavior was negatively related to follower performance for leaders with low LMX (1 SD below the mean; $B = -0.11$, SE = 0.05, $t = -1.94$, $p = 0.054$, 95% CI [−0.21, 0.00]), but not for leaders with high LMX (1 SD above the mean; $B = 0.06$, SE = 0.07, $t = 0.88$, $p = 0.380$, 95% CI [−0.07, 0.19]).

Finally, we found support for a conditional indirect effect of leader narcissism on follower performance *via* perceptions of inconsistent leader behavior moderated by leader gender and LMX (Hypothesis 4) as the index of moderated mediation was significant, which means that the indirect relationship of leader narcissism with follower performance through inconsistent leader behavior was found to be a function of gender and LMX (Index = 0.0537, SE = 0.03, 95% CI [0.001, 0.135]). As predicted, for female leaders with low LMX (1 SD below the mean), leader narcissism was negatively related to follower performance through perceptions of inconsistent leader behavior ($B = -0.08$, SE = 0.04, 95% CI [−0.169, −0.002]). For female leaders with high LMX (1 SD above the mean), the negative relationship between inconsistent leader behavior and follower performance became insignificant and the indirect relationship was no longer there ($B = 0.04$, SE = 0.04, 95% CI [−0.040, 0.138]). For male leaders there was no indirect negative relationship between leader narcissism and follower performance through perceptions of inconsistent leader behavior, both when they had low LMX (1 SD below the mean; $B = -0.01$, SE = 0.02, 95% CI [−0.053, 0.021]) as well as when they had high LMX ($B = 0.01$, SE = 0.01, 95% CI [−0.019, 0.038]), providing further support for Hypothesis 4. See **Figures 2, 3** for the interaction effects. Results of the moderated mediation analysis are presented in **Table 3**.

DISCUSSION

In this paper, we aimed to contribute to the narcissism, gender, and the leadership literature by specifying a mechanism through which leader narcissism might influence follower performance, namely, perceived inconsistent leader behavior, and identifying gender as a moderator. Previous work shows that narcissists have the tendency to be impulsive and feel entitled to change their minds on a whim and that narcissistic leaders are evaluated differently based on their gender. To date, an explanation for these gender differences is lacking. To address this, we drew from the literature on narcissism and leadership and proposed a moderated mediation model in which the relationship of

TABLE 2 | Means, standard deviations, and correlations (Cronbach Alphas on diagonal).

	M	SD	1	2	3	4	5	6	7
1. Follower gender	1.50	0.50							
2. Leader gender	1.38	0.49	0.41**						
3. Leader tenure with follower	3.86	4.63	−0.02	−0.18*					
4. Leader narcissism	3.82	0.86	−0.08	0.00	−0.07	(0.85)			
5. ILB	2.66	1.35	−0.03	0.05	−0.05	0.21**	(0.87)		
6. LMX	5.40	0.91	0.09	0.08	0.08	−0.15*	−0.46**	(0.87)	
7. Follower performance	5.95	0.72	0.08	−0.05	−0.01	0.00	−0.16*	0.22**	(0.87)

N = 165 (150 for tenure). Tenure in years. Men are coded as 1, women are coded as 2. ILB, Inconsistent leader behavior, and LMX, Leader–member exchange.
$^*p < 0.05$; $^{**}p < 0.01$.

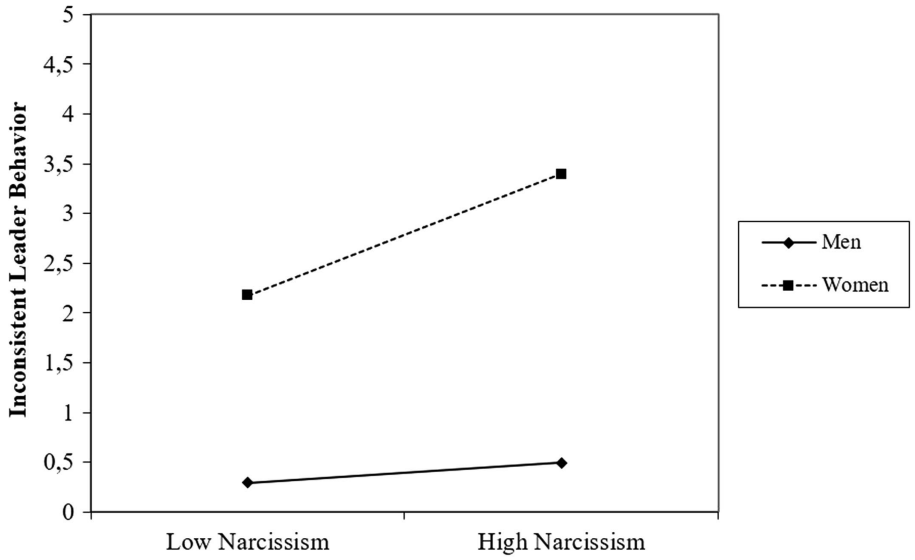

FIGURE 2 | Effect of leader narcissism and leader gender on follower perceptions of inconsistent leader behavior.

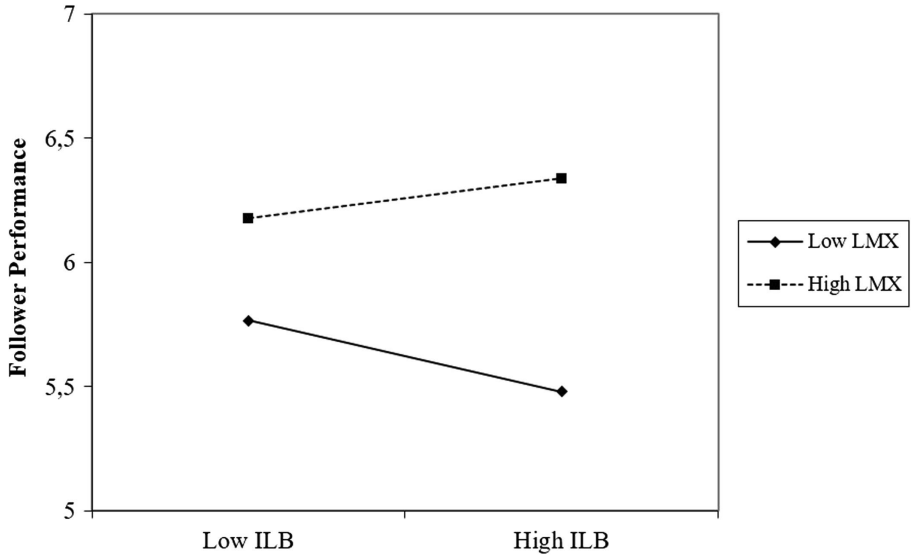

FIGURE 3 | Effects of follower perceptions of inconsistent leader behavior (ILB) and quality of the leader-follower relationship (LMX) on follower performance.

leader narcissism with follower performance is mediated by perceived inconsistent leader behavior.

We expected the effect of leader narcissism on perceptions of inconsistent leader behavior to depend on leader gender. Also, we expected the effect of perceptions of inconsistent leader behavior to depend on the quality of the relationship between the leader and the follower. In a multi-source field study, we found support for the expected gender differences. Specifically, we found that leader narcissism was indirectly negatively related to follower performance *via* perceived inconsistent leader behavior, but only for followers of female leaders who experience low LMX. This suggests that a high-quality relationship may act as a buffer for the potential negative effects of narcissism and perceived inconsistent leader behavior, specifically for female leaders.

Theoretical Implications

Our research contributes to the gender literature by further developing insights into why the effects of leader narcissism and follower outcomes tend to differ between men and women. Specifically, we found that female narcissists are perceived as displaying more inconsistent behavior, and this may be one explanation for inconclusive findings in evaluations of narcissistic leaders. Prior research showed that narcissists are more impulsive (Vazire and Funder, 2006) and opportunistic (Konrath et al., 2016). Here we show how these characteristics seem to translate

TABLE 3 | Results of the moderated mediation analysis using the PROCESS macro 21.

Predictor	*B*	*se*	*t*	(95% CI)
Inconsistent Leader Behavior				
Constant	−0.00	0.10	−0.00	(−0.20, 0.20)
Predictors				
Leader narcissism	0.34**	0.12	2.91**	(0.11, 0.58)
Leader gender	0.14	0.21	0.67	(−0.27, 0.55)
Leader narcissism * Leader gender	0.59*	0.24	2.41*	(0.10, 1.07)
Follower performance				
Constant	0.05	0.06	0.85	(−0.07, 0.17)
Predictors				
Leader narcissism	0.04	0.07	0.55	(−0.09, 0.16)
ILB	−0.02	0.05	−0.49	(−0.12, 0.08)
LMX	0.11	0.07	1.50	(−0.03, 0.25)
ILB * LMX	0.09*	0.04	2.11*	(0.01, 0.18)
Index ILB	0.0537*	0.035		(0.001, 0.135)

N = 165.
*$p < 0.05$; **$p < 0.01$.

into female narcissistic leaders being perceived as behaving inconsistently in the leadership role, which is experienced negatively by followers. Our research adds to the stream of research on gender differences and judgment (e.g., Sherif and Hovland, 1961) by showing that the negative aspects of narcissism in terms of being divergent and unpredictable seem to be more salient for women. Such behavior is incongruent with people's stereotypes about women and thus perceptually contrasted from these stereotypes (see also Manis et al., 1988). For men, agentic behaviors, such as being dominant and erratic, do not seem to be incongruent and do not come with a backlash. However, this backlash effect does happen for women: the contrast with gender expectations does seem to translate into negative evaluations. This new negative and gendered pathway from leader narcissism to follower performance aids in explaining differences in the relationship of narcissism and leader effectiveness for men and women (De Hoogh et al., 2015).

Furthermore, we answer the call for more research into behavioral inconsistency and related constructs (Simons, 2002) by looking into both antecedents and outcomes of perceptions of inconsistent leader behavior. Although varying leader behavior has been studied previously, it was usually studied from a positive perspective (how leaders vary behavior in order to be flexible or adapt to the situation or person), narrowed down to a specific type of inconsistency (e.g., word-deed alignment; Dineen et al., 2006), or focused on displaying two different leadership styles simultaneously (e.g., Vullinghs et al., 2020). Here, we contribute theoretically by showing that perceptions of overall inconsistent behavior form a broad construct that seems to be negatively related to follower performance.

Managerial Implications

Our research findings show that it is important to pay attention to gender effects. Because agentic traits are to some extent deemed necessary to be able to make it at the top (Eagly and Karau, 2002) researchers have previously focused on potential "buffers" for the effects of non-stereotypical gender behavior. Even in leadership roles, gender differences exist along the communal dimension (Moskowitz et al., 1994) as female leaders show empathy and build relationships more readily than their male counterparts (Fletcher et al., 2000). For female leaders, it seems that being high on agentic traits might be accepted as long as those traits do not conflict with the prescription for women of being kind and displaying communal behavior (Prentice and Carranza, 2002). This suggests that displaying desirable communal behavior might prevent negative outcomes. In our study, we find that indeed female narcissistic leaders can make up for their display of counter stereotypical agentic behavior by forming high-quality interpersonal relationships with subordinates.

Since a high-quality relationship mitigates negative effects of perceptions of inconsistent leader behavior, regardless of the gender of the leader, organizations should think of ways to help leaders to improve the relationships with their followers. Providing support and displaying loyalty and trust characterize a high-quality LMX (Graen and Scandura, 1987; Uhl-Bien and Maslyn, 2003) and explicit attention to supporting followers could therefore help in improving the quality of leader–follower relationships. Furthermore, leaders might provide more rationales for their behaviors because explanations for behavior can positively influence the perception and interpretation of leader behavior by followers (Simons, 2002). Transparency might thus help to minimize problems of inconsistent leader behavior.

Finally, our findings provide valuable insights into the overrepresentation of male leaders and how this might relate to (toxic) workplace cultures. While research on narcissism has established a positive link between narcissism and leader emergence as well as leadership ratings (e.g., Brunell et al., 2008; Nevicka et al., 2011a), our results suggest that particularly men might profit from this. Whereas female narcissistic leaders experience backlash, our findings suggest that narcissism is more readily accepted in male leaders allowing them to occupy leader positions, typically accompanied by power. As leaders form role models for followers, agentic and unpredictable behavior shown by narcissistic male leaders might be seen as acceptable and hence "rub off," thereby potentially creating a negative culture of inconsistency.

Limitations and Future Research Directions

Despite its contributions, we recognize that our study has limitations. First, even though we use a multi-source design and focus on leader trait narcissism, a personality characteristic, as our independent variable and behaviors as mediators and outcome variable, our research design was cross-sectional, which means we cannot draw firm conclusions about causality. Also, we used a non-probability sampling method which might limit the generalizability of our findings. Future research should consider studying the variables in an experimental setting and use a more systematic sampling approach.

In future studies, it will be important to investigate the specific mechanisms expected to underly the gender differences,

namely, gender role expectations. We do find that female narcissistic leaders are perceived as more inconsistent, however, we cannot conclude with certainty that this is explained by what behavior followers expect from their leaders as we did not measure such gender role expectations. Gender role expectations may also differ depending on industry. For example, the positive relationship between leader narcissism and perceived inconsistent leader behavior might be even stronger in more stereotypical female industries (e.g., healthcare) as compared to stereotypical male industries (e.g., finance). We would advise future researchers to look into these underlying mechanisms.

Third, inconsistent behavior should be also investigated over time as a specific display of behavior will be perceived as inconsistent when differing from behavior displayed earlier in time. Therefore, in addition to studying inconsistent behavior cross-sectionally, we would encourage future researchers to look into ways of studying inconsistent leader behaviors longitudinally, for example through experience sampling.

Next, we used a new measure of inconsistent leader behavior, thereby advancing research. However, we encourage researchers to further look into our new scale and further test and extend it. Future research on different dimensions of inconsistent leader behavior could yield compelling insights regarding whether or not some dimensions (e.g., relation-oriented behaviors) send more inconsistent cues than others (e.g., task-oriented behaviors). Furthermore, it would be interesting to take also follower personality into account when looking into the effects of inconsistent leader behavior to see who is better able to deal well with an inconsistent leader and which individuals suffer most.

Further, as we measured performance as a leader rating, it may be possible that this rating is biased by the quality of LMX, where leaders see the followers with whom they have high LMX as performing well. That said, the 0.22 correlation is very similar to the 0.24 overall correlation found in a meta-analysis between LMX and objective measures of performance (see Martin et al., 2016). Also, the rating of follower performance might be biased by leader's narcissism, potentially in combination with LMX: narcissistic leaders "punish" followers with whom they have low LMX through lower performance evaluations. While we collected multi-source data and did not find a significant correlation between leader narcissism and leader's rating of follower performance, we did find a significant positive correlation between LMX and follower performance. To avoid this potential bias, future research should collect objective data on follower performance or use performance ratings from different sources (e.g., 360-degree feedback or peer evaluations).

Also, in this study, we focused on the moderating effect of LMX on the relationship between perceived inconsistent leader behavior and follower performance. However, followers perceiving their leader to display inconsistent behavior might in turn like the leader less (i.e., a decrease in the quality of the relationship between leader and follower) and may lower their job performance, which would suggest that LMX mediates the relationship between perceived inconsistent leader behavior and follower performance. Even though we acknowledge that there might be a direct relationship between perceived inconsistent leader behavior and LMX that is most likely negative, we were especially interested in studying the potential buffering effect of LMX. Such focus on the quality of LMX as a moderator is theoretically supported by earlier research showing that LMX influences the link between leader behavior and follower reactions to this behavior (Piccolo and Colquitt, 2006; Michel and Tews, 2016). However, it would still be interesting to study the direct relationship between perceptions of inconsistent leader behavior and LMX. Also, future research could study the potential pathways through which leader narcissism negatively affects LMX (e.g., because narcissistic leaders might generally show less prosocial behavior toward followers).

Finally, it would be of interest to find out whether leader inconsistency can possibly also have positive outcomes. Literature suggests that (narcissistic) leaders strategically act in ways that imply low self-control, because power is associated with the freedom to act according to one's own volition (Hart et al., 2017). Studies suggest that violating (social) norms indeed fuels perception of power (Van Kleef et al., 2011, 2012). It might be that the agentic traits related to narcissism are perceived as powerful and dominant for male narcissistic leaders, but not or less so for women. This forms an interesting area of research.

CONCLUSION

Leader narcissism is evaluated both positively and negatively. Our research provides an explanation for a negative effect of leader narcissism on follower performance by showing that female narcissistic leaders tend to be perceived to show inconsistent behavior, and such behavior relates negatively with performance for followers who have a low-quality relationship with their leader. These results highlight that leaders being perceived as displaying behavioral inconsistency can be a problem, and that gender is an important factor to consider for further studies on this topic.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Economics & Business Ethics Committee (EBEC). The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

EG, AH, DH, and FB contributed to conception and design of the study. EG and AH performed the statistical analysis. EG wrote the original draft. All authors contributed to the article and approved the submitted version.

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Reaching the top but not feeling on top of the world: Examining women's internalized power threats

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More and more women are breaking the glass ceiling to obtain positions of power. Yet with this rise, some women experience threats to their power. Here we focus on women's perceived threats to the stability of their power and the degree to which women feel they do not deserve their power positions, as reflected in their impostor feelings. The present research identifies key workplace characteristics that are associated with these internalized power threats with survey data collected among 185 women in high-power positions. We find that negative workplace experiences (i.e., gender discrimination, denigrating treatment, lack of cultural fit, and lack of mentoring) are associated with a greater sense of power threat, which in turn relates to adverse workplace outcomes (i.e., reduced job satisfaction and increased emotional exhaustion and opting-out intentions). With this unique sample of high-powered women, our findings help illustrate the forces that make women experience power as precarious, thereby shedding light on the disadvantages these women face. We provide suggestions on how to reduce women's internalized power threats.

KEYWORDS

power threat, instability, impostor phenomenon, gender, impostor feelings

Introduction

More and more women are breaking the glass ceiling to obtain positions of power (ILO, 2020; OECD, 2022). With this rise, it seems vital to fully understand how women experience their power. Although possessing and experiencing power has traditionally been associated with positive outcomes (e.g., less stress, more action and optimism; Anderson and Berdahl, 2002; Keltner et al., 2003), more recent research points to important drawbacks, especially for women (Kark et al., 2021; Vial et al., 2022), and especially when one's power is threatened (Scheepers et al., 2015). Indeed, research has shown that the fear of losing one's power and the fear of not deserving one's power position, that is, impostor feelings or

impostor phenomenon (Clance and Imes, 1978), are associated with increased stress (Jordan et al., 2011; Feenstra et al., 2017), anxiety (Cokley et al., 2015), and being distrustful of other people (Mooijman et al., 2019; Feenstra et al., 2020b). These detrimental consequences raise the question of which factors are associated with women's internalized power threats.

To date, we cannot fully answer this important question. Although much is known about the struggles women face when climbing the power ladder, for example, being discriminated against, excluded from informal networks, lesser feelings of "fitting in," and lack of mentoring opportunities (Lyness and Thompson, 2000; Peters et al., 2012; Ellemers, 2014; Begeny et al., 2020), we know relatively little about what happens once women obtain such positions of power. Prior research in this realm has focused on how others perceive powerful women (Eagly et al., 2000; Heilman, 2012; Vial et al., 2016; Ellemers, 2018), but scholars have paid less attention to women's own perceptions and experiences of obtaining positions of power.

The present research aims to fill this gap and identifies workplace experiences that are associated with internalized threats to women's power. In doing so, we build on a wealth of research that has documented specific barriers that women face during their career, and specifically on their paths to power (e.g., Lyness and Thompson, 2000; Hoyt, 2010; Sue, 2010). These workplace experiences include being discriminated against because of one's gender (Albrecht et al., 2003; Heilman and Caleo, 2018), being interrupted or 'cut off' when sharing an idea (Begeny et al., 2021a), being excluded from informal networks (Lyness and Thompson, 2000; Durbin, 2011), and lacking mentoring opportunities (Bogat and Redner, 1985; Lyness and Thompson, 2000). Here we propose that these workplace experiences not only impact women on their paths to power, but also have detrimental consequences once these women reach the top, by shaping their sense of power threat. Thus, our first aim in the present research is to show that the negative workplace experiences of women when climbing the power ladder (i.e., gender discrimination, denigrating treatment, and lack of cultural fit and mentoring) are associated with heightened perceptions of power threat. Our second aim is to show that these internalized power threats, in turn, are related to negative workplace outcomes, such as, reduced job satisfaction and organizational identification, and increased emotional exhaustion and opting-out intentions (see Figure 1).

Overall, the present research contributes to our understanding of how women experience positions of power. While prior research primarily focused on identifying detrimental consequences of external power threats (e.g., Maner and Mead, 2010; Williams, 2014; Neureiter and Traut-Mattausch, 2016), we add to this work by explaining why some women themselves feel that their power is threatened in the first place. In doing so, our work raises important theoretical and practical considerations that could help reduce internalized power threats among women, ultimately making them more comfortable and secure with their power.

Theory

The concept of internalized power threats

Power is defined as asymmetric control over valued resources, such that people with higher power control valued resources, while those with lower power are dependent on others for such resources (Magee and Galinsky, 2008). Power is a positive state and therefore powerholders are generally very attentive to potential threats to their power (Williams, 2014). Here, we focus on two types of

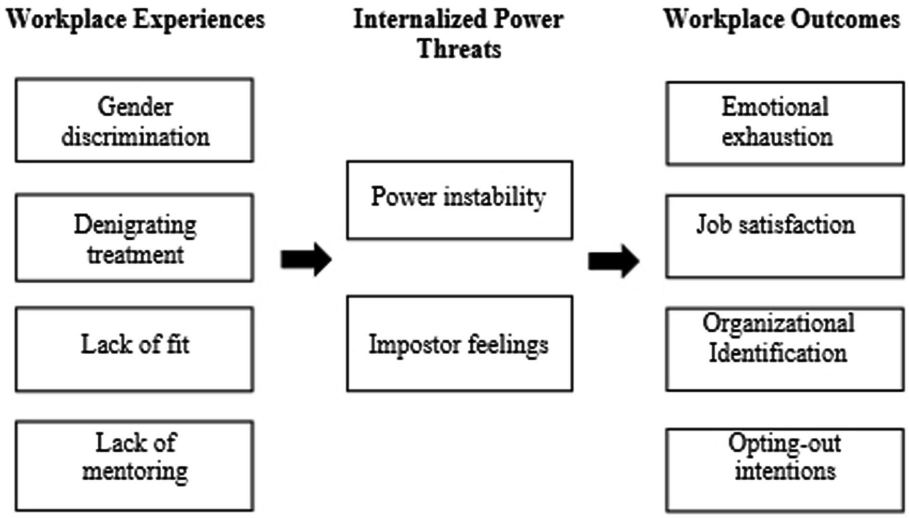

FIGURE 1
Conceptual model of workplace experiences, internalized power threats, and workplace outcomes. The constructs outlined in the figure are illustrative of the overarching factors of workplace experiences and workplace outcomes.

internalized power threats that women are likely to experience: perceived threats to the stability and deservingness of their power.

First, we focus on stability, that is, the fear of losing power. This type of power threat derives from the fact that power is dynamic. Power relationships can change, such that powerless individuals can climb the power ladder, and the powerful can lose their control over valued resources, descending down the ladder. Being in an unstable power position is stressful, and greatly impacts individuals' well-being and behavior (Maner and Mead, 2010; Jordan et al., 2011; Scheepers et al., 2015; Feenstra et al., 2017; Feenstra et al., 2020b).

Second, we focus on the extent to which powerholders feel that they do not deserve their power positions. An important phenomenon in this regard is the impostor phenomenon, which refers to feelings that one has received power not because of personal merits or achievements, but due to luck or coincidence. Hence, these individuals tend to feel like impostors and worry that they will be "found out." This phenomenon was first described in 1978 by clinical psychologists Clance and Imes, who pointed out that high-achieving women were unable to internalize and accept their success and attributed their accomplishment to external factors instead. Although more recent research shows that men can also feel like impostors (Bravata et al., 2019), the phenomenon is more often associated with the experiences of *women* in high-power positions (Meister et al., 2017).

We conceptualize and operationalize these experiences as *internalized* threats to a person's (in this case women's) power. In other words, we focus on women's own perceptions of, and experiences with, power. We further propose that this internalized sense of threat is – at least to some degree – rooted in external (contextually-relevant) factors, including others' actions toward them. This proposition aligns with other theory and research on group processes, which suggest that how individuals view and think about themselves is shaped by external forces (e.g., others' actions towards them; for relevant discussions, see, e.g., Huo and Binning, 2008; Feenstra et al., 2020a).

Workplace experiences and power threats

In the present research, we aim to understand why some women experience threats to their power. Specifically, we build on a wealth of research that has identified specific challenges women face on their paths to power (e.g., Lyness and Thompson, 2000; Hoyt, 2010; Sue, 2010). The first is that women are often discriminated against because of their gender. Compared to men, women are, for instance, evaluated more harshly (Heilman and Caleo, 2018; Begeny et al., 2021b), less likely to be hired for management positions (Gorman, 2005), and paid less for the same work (Bishu and Alkadry, 2017; Catalyst, 2018). Such experiences signal to women that the system is not fair and that important outcomes are beyond their control (Major and Crocker, 1993). This ultimately hurts their psychological well-being (Schmitt et al., 2003). Building on this work, we argue that having been and being subject to discrimination is likely to elicit doubts among women about the continuity of, and their suitability for powerful positions. Overall, we thus propose that women who face gender discrimination on their paths to power will be more likely to feel that their power is threatened.

In addition to overt gender discrimination, women are also likely to encounter more subtle struggles on their paths to power (Lyness and Thompson, 2000). In this regard, research has shown that women are more likely than men to experience denigrating treatment from their colleagues and supervisors, such that they are more likely to be interrupted, criticized, or have their contributions overlooked (for a review see Begeny et al., 2021a) compared to their male counterparts. Such seemingly trivial interactions at work actually communicate that the target is not seen as a person of value or worth and that their insights are valued less compared to that of others (Holleran et al., 2011). Ultimately, such denigrating treatment is important in shaping individuals' sense of self-worth and potentially, their impostor feelings (Tyler and Blader, 2003; Feenstra et al., 2020a). As such, we argue that being the target of denigrating treatment is likely to be positively associated with experiencing power threats.

Furthermore, previous research demonstrates that women are less likely to feel that they fit in their places of work and report that this lack if fit is an important barrier in climbing the corporate ladder (Lyness and Thompson, 2000; Peters et al., 2012). Research suggests that women are particularly likely to experience such lack of fit in masculine organizational cultures and male-dominated professions (Heilman and Caleo, 2018). Peters et al. (2012), for instance, showed that female trainee surgeons experienced a greater lack of fit with the masculine surgeon prototype than male trainees. Such lack of fit, in turn, causes women to feel out of place and question their own power (Feenstra et al., 2020b; Kark et al., 2021). In corroboration with these arguments, we propose that women's experiences with a lack of fit are positively associated with experiencing power threats.

Finally, considering the negative experiences of women in the workplace, research suggest that mentoring is essential to women's career advancement (Tharenou, 2005). Given that women are underrepresented in higher echelons of organizations, however, there are fewer role models and mentoring opportunities available for women who aspire to high-power positions (Bogat and Redner, 1985; Lyness and Thompson, 2000). Research suggest that missing-out on such an important resource of mentoring would likely shake women's confidence and spur their impostor feelings (Ehrich, 2008; Sanford et al., 2015). As such, we argue that a lack of mentoring opportunities is positively associated with experiencing internalized power threats.

Taken together we thus hypothesize:

> *H1:* Negative workplace experiences (i.e., gender discrimination, denigrating treatment, and a lack of fit and mentoring) are positively associated with women's internalized power threats (i.e., perceptions of power instability and impostor feelings).

Outcomes of power threats

In a next step, we aim to show that these internalized power threats are associated with detrimental workplace outcomes. First, we build on a wealth of theorizing and empirical support to argue that power threats can harm mental health and shape women's stress experiences. Indeed, the conservation of resources theory (Hobfoll, 1989) argues that one of the main sources of stress is "when individuals' resources are threatened with loss" (Hobfoll, 2001, p. 342). In support of such theorizing, empirical studies found that both power instability and impostor feelings are associated with increased stress and anxiety (Sonnak and Towell, 2001; Jordan et al., 2011; Feenstra et al., 2017). Here, we focus on a particularly salient stress experience in the work context, namely burnout. Specifically, we will focus on the core component of burnout which is emotional exhaustion. Emotional exhaustion refers to the experience of feeling "empty" (Maslach et al., 2001; Seidler et al., 2014). Building on the work described above, we argue that women's internalized power threats are likely to be associated with heightened emotional exhaustion.

In addition to the psychological well-being of female powerholders, other important workplace outcomes that are likely to be related to power threats relate to the enjoyment of, and commitment to, their work. In this domain, researchers have argued that women who experience a lack of career prospects enjoy their work less, are less committed, and more likely to "opt-out" of their organization (Ellemers, 2014). Because of their expectation that they might not get ahead, or are likely to lose their positions and resources, these women are, for instance, less likely to make sacrifices for their work (Meeussen et al., 2021). Consistent with this reasoning, seminal empirical work showed that feelings of impostorism are indeed related to reduced job satisfaction and lack of commitment (Vergauwe et al., 2014; Neureiter and Traut-Mattausch, 2016). Building on this research, we argue that concerns about the stability and deservingness of one's power are negatively associated with women's work satisfaction and identification, and positively associated with their intention to "opt-out." Overall, we hypothesize:

> *H2:* Women's internalized power threats (i.e., perceived power instability and impostor feelings) are positively associated with emotional exhaustion and opting-out intentions, and negatively associated with job satisfaction and organizational identification.

Materials and methods

You can find more information about our sample, measures, and data analysis in the Supplementary materials here. This study was not preregistered. Participants of this study did not agree for their data to be shared publicly, so supporting data is not pubicly available.

Participants and procedure

We approached women who were affiliated with an international women's networking organization that offered leadership development programmes and conferences for its members. We contacted potential participants *via* e-mail to complete an online survey about their experiences in their organizational workplaces. In total 343 potential participants clicked our survey link, of which 241 responded to all key variables (i.e., negative workplace experience and power threat items). Because we focus on women's experiences of power in this study, we excluded 11 male participants and 45 women who did not occupy a management position[1]. Hence, we conducted our final analysis using 185 women (response rate = 54%; *M*age = 45.45; *SD* = 7.99) from various countries, such as Switzerland (31.9%), United Kingdom (9.2%), and Japan (5.9%). Participants were highly educated, with more than 70% having obtained a Master's degree or higher. Women reported working in sector such as information technology (16.8%), marketing, sales, and service (8.1%), finance (6.5%), or agriculture, food, and natural resources (7%). Moreover, these women held positions of substantial power in their organizations and institutions, with most of the participants representing either top-management (34.1%) or middle-management positions (54.1%) and supervising up to 20 employees (79%) or more (21%). Though standards for power analyses to test models in SEM are less well-established, the proportion of latent factors to manifest variables specified to test key hypotheses (3 to 10) suggest that we required a sample size of 156 to detect a medium sized effect, or larger ($\alpha = 0.05$, $1 - \beta = 0.80$; conventionally, r of.10/0.30/0.50 is considered small/medium/large effect; Soper, 2022). Overall, this indicates that this study is well powered.

Measures

Our survey was part of a wider data collection effort. In the Supplementary materials we included a list of additional measurements that were not included here.

Workplace experiences

First, we asked participants about negative workplace experiences throughout their career. To measure gender discrimination, we asked participants how often during their career they felt that they were: deprived of certain opportunities (available to others) because of their gender, treated according to stereotypes based on their gender, discriminated against because of their gender, and, viewed negatively because of their gender

1 We note that conducting the main analysis reported below using a sample including these 45 women in non-management positions, did not meaningfully change any of the reported findings. See Table 6 in the supplementary material for the full results.

(Bongiorno et al., 2021; $\alpha = 0.92$). Participants responded to these four items on a scale from 1 (*never*) to 5 (*very often*). We further asked participants to think about the people they interacted with at work (i.e., their co-workers, supervisors, other employees). Following Begeny et al. (2021a) we then measured denigrating treatment by asking how often these people interrupted them or 'cut them off' when they were trying to share an opinion or idea, drew attention to relatively minor errors or mistakes they made, seemed to overlook the contributions they made to the organization, and left them out of conversations, group emails, or other informal meetings/gatherings/discussions ($\alpha = 0.77$). Participants responded to these four items on a scale from 1 (*never*) to 5 (*very often*).[2] Finally, following Lyness and Thompson (2000), we measured lack of fit with three items ($\alpha = 0.77$) and lack of mentoring with four items ($\alpha = 0.86$). We asked participants the extent to which they experienced the following throughout their career: felt pressure to fit in or adapt to the organizational culture, had few role models, felt like they were an outsider (i.e., lack of fit) and not having enough mentoring (e.g., counselling about career opportunities), not having a senior manager who facilitates their career progress, not getting access to the right people (or not knowing the right people), and not receiving enough meaningful feedback about their strengths and weaknesses (i.e., lack of mentoring). Participants responded to these items on a scale from 1 (*not at all*) to 5 (*to a very great extent*).

Internalized power threats

We measured power instability by asking participants to indicate the extent to which they felt that their position, status, authority, and power were threatened – a possibility that it will get worse in the future (Feenstra et al., 2020b; $\alpha = 0.96$). Participants responded to all 4 items on a scale from 1 (*not at all*) to 5 (*to a very great extent*). Furthermore, we measured impostor feelings with the 7-item impostorism scale developed by Leary et al. (2000; $\alpha = 0.92$). An example item was: "I'm afraid important people at my work may find out that I'm not as capable as they think I am."

Workplace outcomes

We measured job satisfaction with two items taken from Hackman and Oldham (1980). The items were: "Generally speaking, I am very satisfied with my job" and "I am generally satisfied with the kind of work I do in my job" ($r = 0.62$, $p < 0.001$, $\alpha = 0.76$). We further measured emotional exhaustion with 3-items from the Maslach Burnout Inventory (MBI; Maslach et al., 1996). The items were: "I feel emotionally drained from my work," "I feel burned out from my work," and "I feel fatigued when I get up in the morning and have to face another day on the job" ($\alpha = 0.80$). Additionally, we measured organizational identification with six items developed by Mael and Ashforth (1992; $\alpha = 0.87$). An example item is: "My organization's successes are my successes." Finally, we measured opting-out intentions by asking participants to what extent they disagreed or agreed with the statement "I often think about quitting my job" (Mobley, 1977). For all outcomes, participants responded on a scale from 1 (*strongly disagree*) to 5 (*strongly agree*).

Potential control variables

We considered participants' age (in years), educational level (1 = did not complete high school, 2 = high school, 3 = some college, 4 = bachelor degree, 5 = master degree, 6 = advanced graduate work or PhD), management level (1 = lower, 2 = medium, 3 = top), number of employees they supervised (1 = no, 2 = 1–5, 3 = 6–10, 4 = 11–15, 5 = 16–20, 6 = more than 20), hierarchical power level (from 1[bottom] to 100 [top]; Lammers et al., 2010), and the gender dominance of the sector in which they worked (dummy coded; dummy 1 [0 = mixed/female-dominated, 1 = male-dominated] and dummy 2 [0 = mixed/male-dominated and 1 = female-dominated]; Mroczek-Dąbrowska and Gaweł, 2020), as potential control variables as previous research suggested that these are associated with our outcome variables (Thompson et al., 2000; Vergauwe et al., 2014; Cokley et al., 2015; Feenstra et al., 2020a; Kark et al., 2021).

Results

We analyzed our data using IBM SPSS Statistics Version 27 and used SPSS AMOS for structural equation modelling (SEM).

Factor structure

We conducted confirmatory factor analyses (CFAs) to examine how the data fitted our three-factor model, with workplace experiences, internalized power threats, and workplace outcomes as correlated latent factors and no indicator cross-loadings permitted. Negative workplace experiences was measured by mean scores of gender discrimination, denigrating treatment, and lack of fit and lack of mentoring. Internalized power threat was measured by mean scores of power instability and impostor feelings. Finally, workplace outcomes was measured by mean scores of emotional exhaustion, job satisfaction, organizational identification, and the original score of opting-out intentions. This model showed poor fit to the data ($\chi^2[32] = 76.75$, $p < 0.001$, CFI = 0.91, RMSEA = 0.09, TLI = 0.87), even though all the respective items loaded significantly on their latent variables (all $p < 0.001$). In an effort to improve the fit of

2 For exploratory reasons, we also included a measure of *positive* treatment (3 items; $\alpha = 0.82$; Begeny et al., 2021a). As the present research focuses on the association between *negative* workplace experiences and internalized power threats, we did not include this measure in the main analysis reported below. We note, however, that positive treatment was not associated with power instability ($r = 0.06$, $p = 0.45$), nor impostor feelings ($r = -0.13$, $p = 0.09$). We further note that adding positive treatment as an additional indicator of workplace experiences to the main analysis reported below does not meaningfully change any of the reported findings.

the model, we excluded organizational identification from measuring workplace outcomes, as it was the weakest estimate of all latent factors. This three-factor model did show acceptable fit to the data ($\chi^2[24] = 50.51$, $p = 0.001$, CFI = 0.94, RMSEA = 0.08, TLI = 0.91) and all of the respective items loaded significantly on their latent variables (all $p < 0.001$). Furthermore, this three-factor model had a better fit to the data than a one-factor model (in which all constructs loaded on the same latent variable; $\Delta\chi^2$ (3) = 69.88, $p < 0.001$), a two-factor model (in which all negative workplace experiences loaded on one factor and power threats and workplace outcomes loaded on one factor; $\Delta\chi^2$ (2) = 14.43, $p < 0.001$), a four-factor model (in which the two internalized power threats loaded on separate latent factors; this model was unidentified), and a second-order model (in which the latent factors workplace experiences, internalized power threats, and workplace outcomes were measured by their latent constructs, which we operationalized by their respective items; this model was also unidentified).

Descriptive statistics

Table 1 reports the descriptive statistics. As expected, all negative workplace experiences (i.e., gender discrimination, negative treatment, lack of fit, lack of mentoring) were positively associated with our two measures of internalized power threats (i.e., power instability and impostor feelings). Furthermore, both internalized power threats were positively associated with emotional exhaustion and opting-out intentions and power instability was negatively associated with job satisfaction. Contrary to expectations, neither of the internalized power threats were associated with organizational identification. Considering these observations and the reduced fit of the model when including organizational identification, we excluded this outcome variable in the main analysis reported below.

Model testing

We conducted structural equation modeling using maximum likelihood method to test our predictions. Specifically, we fitted a three-factor model, with workplace experiences, internalized power threats, and workplace outcomes as latent factors (see Figure 2). We modeled a direct path between workplace experiences and internalized power threats and between internalized power threats and work outcomes. Overall, our path-model showed acceptable fit to the data ($\chi^2[25] = 53.93$, $p = 0.001$, CFI = 0.93, RMSEA = 0.08, TLI = 0.91).[3] All mean-leveled constructs loaded significantly on their respective latent variable ($p < 0.001$). Moreover, our hypotheses were supported such that negative workplace experiences were positively associated with internalized power threats (estimate = 0.73, *SE* = 0.09, 95% CI [0.55, 0.91]), which in turn were positively associated with workplace outcomes (estimate = 0.75, *SE* = 0.08, 95% CI [0.55, 0.91]). We note that an alternative model with a direct path between workplace experiences and workplace outcomes and, respectively, between workplace outcomes and power threats had poor fit ($\chi^2[25] = 64.89$, $p < 0.001$, CFI = 0.91, RMSEA = 0.09, TLI = 0.87), suggesting our proposed order of variables is also supported. We further note that including a direct path from workplace predictors to workplace outcomes did not significantly improve the fit of the model, $\Delta\chi^2$ (1) = 3.42, p is between.10 and.05, suggesting that power threats can adequately explain the relationship between workplace predictors and outcomes. Indeed, results showed that internalized power threats mediate the relationships between workplace predictors and outcomes (estimate = 0.54, *SE* = 0.09, 95% CI [0.35, 0.70], $p = 0.01$). Finally, including the control variables, age, educational level, management level, number of employees supervised, and sector dominance did not meaningfully change any of the reported associations (see Supplementary Table 7).

Discussion

In this investigation, we examined why some women who have reached the top in organizations experience power threats. We demonstrated that negative workplace experiences, such as denigrating treatment, and lack of fit, are positively associated with fears about the stability and legitimacy of women's power. We further demonstrated that these experiences of internalized power threats are associated with detrimental work outcomes, such as increased emotional exhaustion and intentions to opt-out of one's organization.

By doing so, our research makes several important contributions. First, our findings provide a better understanding of how women experience positions of high power. While prior research identified obstacles women face on their paths to power (e.g., Eagly et al., 2000; Lyness and Thompson, 2000; Heilman, 2012), we show that negative workplace experiences are associated with women's perceptions and experiences of positions, once they have reached the top. Although being in a position of power is often associated with positive outcomes, such as status and optimism (Anderson and Galinsky, 2006; Magee and Galinsky, 2008), our findings suggest that for those women who have had negative workplace experiences, positions of power come with specific challenges. Consequently, our work shows that it is important to not just focus on whether women reach the top, but to also look at how women experience these positions of power once they do.

Second, our findings contribute to the work on power threats more generally, and impostor feelings, in particular. Research on power instability, for instance, primarily examined detrimental

3 Modification indices suggested that model fit could further be improved by including a direct path from job satisfaction to intentions to opt-out. As this path was not part of our initial investigation, we decided not to include it.

TABLE 1 Descriptive statistics.

	M (*SD*)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1. Age	45. 45 (7.99)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2. Educational level	4.70 (0.92)	−0.04	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3. Power level	75.11 (15.57)	0.23**	0.06	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4. Management level	3.22 (0.64)	0.25**	0.07	0.76**	–	–	–	–	–	–	–	–	-	–	–	–	–
5. Employee supervision	3.22 (1.76)	0.23**	−0.14	0.36**	0.29**	–	–	–	-	–	–	–	–	–	–	–	–
6. Sector gender dominance (dummy 1)	0.39 (0.49)	0.08	0.03	0.05	0.06	0.13	–	–	–	–	––	–	–	–	-	––	–
7. Sector gender dominance (dummy 2)	0.21 (0.41)	−0.04	0.03	−0.03	0.01	−0.02	−0.41**	–	–	–	–	–	–	–	–	–	–
8. Gender discrimination	2.48 (0.97)	0.03	0.27**	0.27**	0.33**	0.05	0.20*	−0.10	–	–	–	–	–	–	–	–	
9. Denigrating treatment	2.80 (0.68)	0.04	0.12	0.06	0.18*	−0.02	0.03	0.06	0.48**	–	–	–	–	–	–	–	-
10. Lack of fit	3.01 (0.96)	0.01	0.27**	0.20*	0.24**	−0.06	0.09	−0.124	0.52**	0.43**	–	–	–	–	–	–	–
11. Lack of mentoring	2.99 (1.01)	−0.03	0.24**	−0.03	0.07	−0.13	0.06	−0.06	0.54**	0.36**	0.62**	–	–	–	–	–	–
12. Impostor feelings	1.66 (0.81)	−0.23**	0.11	0.00	0.05	0.04	0.00	−0.07	0.22**	0.25**	0.34**	0.31**	–	–	–	–	–
13. Power instability	2.44 (1.15)	0.03	0.12	−0.13	0.03	−0.11	0.12	−0.06	0.31**	0.38**	0.31**	0.32**	0.23**	–	–	–	–
14. Emotional exhaustion	3.20 (0.85)	0.01	0.11	−0.10	0.04	−0.03	0.10	−0.11	0.29**	0.26**	0.36**	0.23**	0.37**	0.36**	–	–	–
15. Job satisfaction	3.76 (0.88)	0.06	−0.06	0.22**	0.18*	0.19*	−0.07	−0.02	−0.11	−0.25**	−0.14**	−0.20**	−0.09	−0.37**	−0.38**	–	–
16. Organizational identification	3.80 (0.74)	0.13	−0.04	0.24**	0.21**	0.13	−0.05	0.05	−0.03	−0.02	−0.17*	−0.20**	0.01	−0.13	−0.09	0.37**	–
17. Opting out	2.67 (1.23)	−0.04	0.00	−0.06	−0.04	0.07	−0.08	0.03	0.18*	0.23**	0.20**	0.24**	0.19**	0.32**	0.46**	−0.49**	−0.24**

N ranges from 154 to 185. *$p < 0.05$, **$p < 0.01$. For educational level, 1 = Did not complete high school, 2 = High school, 3 = Some college, 4 = Bachelor degree, 5 = Master degree, 6 = Advanced Graduate work or PhD. For management level, 1 = lower management, 2 = middle management, 3 = top management. For employee supervision, 1 = no, 2 = 1-5, 3 = 6-10, 4 = 11-15, 5 = 16-20, 6 = more than 20. For sector gender dominance dummy 1, 1 = male-dominated, 0 = female-dominated and mixed. For sector gender dominance dummy 2, 1 = female-dominated, 0 = male-dominated and mixed.

consequences of unstable power (Jordan et al., 2011; Scheepers et al., 2015; Feenstra et al., 2020b). We contribute to this work by showing the possible origins of such experiences. Furthermore, with regards to impostor feelings, prior research has examined its antecedents, but has tended to focus on *individual* antecedents, such as attachment style or personality of individuals (Bernard et al., 2002; Bravata et al., 2019). Our research takes a different approach, as we adhere to previous calls to examine the role of *context* and the workplace in shaping these experiences (Feenstra et al., 2020a; Kark et al., 2021). In doing so, we contribute to a growing body of work that shows the importance of workplace context in shaping women's impostor feelings (Muradoglu et al., 2022; Vial et al., 2022).

Although we found support for our theorizing that internalized power threats are associated with reduced job satisfaction, increased emotional exhaustion, and opting out intentions, we found no support that these internalized power threats are associated with a drop in women's identification with their respective organizations. This might be because being in a position of high power elicits strong organizational identification, even despite the threats that such high-power roles elicit for

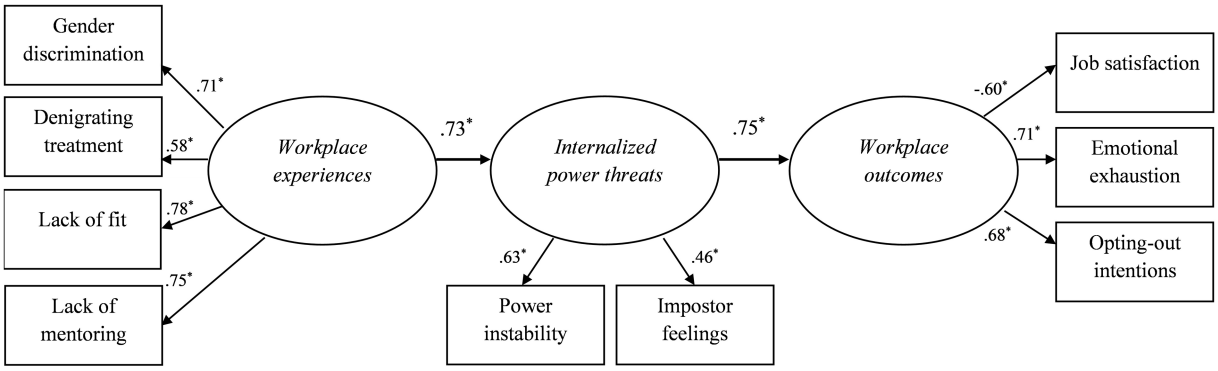

FIGURE 2
Results for hypothesized model. N=185. *p<0.05. Standardized regression weights are reported. Model fit: χ^2[25]=53.93, p=0.001, CFI=0.93, RMSEA=0.08, TLI=0.91.

women. Indeed, prior research has shown that power enhances implicit and explicit role identification (Joshi and Fast, 2013). This explanation should be addressed in future research.

Our research also has important implications for practice. Our findings suggest that to diminish women's perceptions of power threats, it is important to address the workplace experiences that women regularly face in their careers. Instead of focusing on individual interventions, like trying to boost women's self-esteem, our results suggest that it is also relevant to take into account the organizational context, and actively focus on (negative) workplace experiences of women. As such, for women to feel more secure with their power, it is important that more structural issues are addressed, such as reducing gender discrimination and denigrating treatment and increasing women's mentoring opportunities and feelings of fit at work (Ryan, 2022).

This research is not without limitations. Most importantly, the single-source and cross-sectional nature of our data prevents us from identifying cause-and-effect relationships. Hence, it is important that future research replicates our findings using different methods. Researchers could, for example, use multi-sourced data or experimental research designs, manipulating denigrating treatment or lack of fit to test its causal impact on internalized power threats. Furthermore, while our theorizing focused on how women's past experience shape their current sense of power threat, future research could examine how past *and* present experiences sequentially or simultaneously influence women's experience of power. In particular, longitudinal research could help tease out how these processes function over time, and can compare women's career experiences prior to being in positions of power to their experiences when in power. In this regard, future research could, for instance, test a sequential model where women's negative workplace experiences early in their career shape their sense of power threat, which in turn forms their perceptions of current negative workplace experiences as well.

In addition, while the current research identified a first set of contextual factors that shape women's power threat, it is important to recognize that other relevant factors could be at play as well, including other external factors (e.g., organizational climate and culture; Kark et al., 2021), internal factors (e.g., lower levels of trait confidence, anxiety), as well as their interplay. In the latter case, one could imagine, for instance, that especially women with initial lower levels of confidence would question their own power when working in a dysfunctional working environment, while women with higher initial confidence would be shielded more from the negative impact of such potential hurtful contexts.

Future research could further expand this work by examining how women's negative workplace experiences and accompanying power threats impact their leadership behaviours. On the one hand, research in this regard suggests that women's negative workplace experiences and internalized power threats might give them a leadership advantage. Eagly (2007), for instance, argues that female leaders are more likely to show transformational leadership and go beyond the official requirements of their job because of the stereotypes these women face during their career. Similarly, recent research by Tewfik (2022) suggests that female leaders who feel like impostors are more likely to take the perspective of others, and thus will be more effective leaders. On the other hand, there is research arguing that women's negative workplace experiences and internalized power threats may sabotage effective leadership. Vial et al. (2016), for instance, propose that female leaders might end up in a "self-reinforcing cycle of illegitimacy" (p. 400) where a lack of validation of their power, results in aggressive leader behaviour. Similarly, research on power instability, suggests that leaders who fear losing their power will be reluctant to share their power and delegate important decisions to their employees (Feenstra et al., 2020b). Additional research is needed to empirically examine these competing predictions.

We further note that while targeting women involved in a women's international networking organization allowed us access to a hard-to-reach sample of high-powered women, it is possible that women who are affiliated with such an organization have different experiences compared to women who are not members. We could imagine, for instance, that women who experience more

gender discrimination or feel more like impostors would be more likely to join such an organization. It is therefore important that future research replicates the reported findings in other representative high-powered, female, and mixed-gender samples.

Finally, our research was limited to women's experiences with power threats. It would be interesting for future research to examine if, when, and why men feel like their power is under threat and the consequences of this. Probably, men experience less negative workplace experiences and are therefore less likely to experiences these power threats and accompanying negative consequences (Vial et al., 2016). But men might have different contexts in which they are likely to feel like impostors and will likely react more strongly towards threats of their power (Feenstra et al., 2017).

Conclusion

More and more women are breaking the glass ceiling to obtain positions of power. In this study we have shed light on how these women experience positions of high power. Although traditionally power has been associated with numerous benefits, this research demonstrated that for women with negative workplace experiences, power can also come with particular challenges. Our hope is that this work sparks future research that examines women's experiences with power and motivates practitioners to create organizational contexts in which high-powered women will feel like they are rightly on top of the world.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. The patients/participants provided their written informed consent to participate in this study.

Author contributions

SF contributed to conceptualization and data collection, and developed questionnaire, analyzing research data, and wrote manuscript. CB and JJ contributed to conceptualization, developing questionnaire and analyzing data, and reviewed and edited writing. MR, JS, and FR contributed to developing questionnaire, conceptualization and reviewed and edited writing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2022.931314/full#supplementary-material

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Does National Context Matter When Women Surpass Their Partner in Status?

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There is growing evidence that couples in non-traditional relationships in which the woman attains higher status than her male partner experience more negative relationship outcomes than traditional couples. A possible reason is that non-traditional couples violate persisting gender stereotypes that prescribe men to be breadwinners and women to be caregivers of the family. In the current study (N = 2,748), we investigated whether a country's gender-stereotypical culture predicts non-traditional men and women's relationship and life outcomes. We used the European Sustainable Workforce Survey, which is conducted in nine European countries. Two indicators of countries' gender-stereotypical culture are used: Gender Empowerment Measure and implicit gender stereotypes. We found that women's income and -to a lesser extent- education degree relative to their male partner affected outcomes such as relationship quality, negative emotions, and experienced time pressure. Furthermore, men and women living in countries with a traditional gender-stereotypical culture (e.g., Netherlands, Hungary) reported lower relationship quality when women earned more than their partners. Relative income differences did not affect the relationship quality of participants living in egalitarian countries (e.g., Sweden, Finland). Also, couples in which the woman is more highly educated than the man reported higher relationship quality in egalitarian countries, but not in traditional countries. Our findings suggest that dominant beliefs and ideologies in society can hinder or facilitate couples in non-traditional relationships.

Keywords: close relationships, socio-economic status, relationship outcomes, national context, gender stereotypes

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INTRODUCTION

Non-traditional relationships in which women attain higher societal status than their male partners become more common (Pew Research Center, 2013; Portegijs and Van den Brakel, 2018). In almost all western countries, it is nowadays more likely for women to be more highly educated than their male partners (De Hauw et al., 2017). A relationship in which the woman earns more than the man has become more common in recent years (e.g., almost 12% of Dutch women with young children had a higher income than their male partner in 2018 compared to 7% of Dutch women in 2007; Portegijs and Van den Brakel, 2018).

However, non-traditional couples face social and economic penalties as they are perceived more negatively by others (Hettinger et al., 2014; MacInnis and Buliga, 2019; Vink et al., 2021b). Non-traditional couples themselves experience more negative relationship outcomes than couples in traditional relationships (Vink et al., 2021b). When the woman earns more than her husband, both partners tend to be less satisfied with their marriage (Wilcox and Nock, 2006; Bertrand et al., 2015; Zhang, 2015; Syrda, 2019). Moreover, women who work more hours than their male partners report lower relationship quality than women in more traditional relationships (Gong, 2007). Some studies even show that marriages in which the woman is more highly educated than the man are at greater risk of divorce than marriages in which the man is more highly educated (Kalmijn, 2003; Müller, 2003; Goldstein and Harknett, 2006).

It remains unclear why non-traditional couples experience more negative relationship outcomes than traditional couples. Some scholars seek explanations in evolved and universal differences between men and women. They argue that women in general desire partners with good providing skills (e.g., men with high earning potential), whereas men desire partners with good nurturing skills (Buss, 2011). Others argue that it is economically rational if the man is the one who brings home the bacon due to persisting gender inequality in the labor market (Molm and Cook, 1995). However, the differences between men and women are not so stable and are dependent upon the context that they operate in Ellemers (2018). For example, partner preferences are less traditional in countries with a more gender-egalitarian culture (Zentner and Eagly, 2015). Also, couples often fail to make economically rational choices (e.g., women still do the brunt of household tasks, even if they earn more than their male partner; Bittman et al., 2003).

Following this reasoning, we propose that it is more difficult for couples to thrive in a non-traditional relationship in countries with a more traditional gender-stereotypical culture. We define the gender-stereotypical culture as the extent to which social policies and societal norms endorse gender stereotypes, prescribing men to be the breadwinner and women to be the family's primary caregiver. In the current study, we investigate how a country's gender-stereotypical culture is related to relationship outcomes of men and women in relationships in which the woman has higher societal status than her male partner. We add to the existing literature by showing that sociocultural factors at the country level have an important influence on men and women's relationship outcomes in non-traditional relationships.

The Impact of Gender Stereotypes on the Partner in Close Relationships

In order to understand how social policies and societal norms affect countries' gender-stereotypical culture, we first describe how gender stereotypes operate. Cultural norms and expectations dictate suitable characteristics and behaviors for both men and women (Eagly et al., 2000; Heilman, 2001; Prentice and Carranza, 2002). Gender stereotypes follow from observing men and women in typical social roles, such as breadwinning men and caregiving women (Social Role Theory; Eagly, 1987; Eagly et al., 2000). People also expect men to take on higher status roles, whereas they expect women to take on lower status roles (Rudman et al., 2012). Men and women who violate gender stereotypes prescribing that the man should have the higher status role within the relationship are at risk of social penalties (Hettinger et al., 2014; MacInnis and Buliga, 2019; Vink et al., 2021b). Others outside the relationships expect a woman with a higher status profession than her male partner to be the dominant one in their relationship and therefore dislike her (i.e., dominance penalty). Also, they expect a man with lower status than his partner to be the weak one in their relationship and therefore disrespect him (i.e., weakness penalty; Vink et al., 2021b). People expect such non-traditional relationships to be less satisfying for the couple than more traditional relationships (Hettinger et al., 2014; Vink et al., 2021b).

Gender stereotypes also have their impact on partners in close relationships who violate gendered status expectations. Women who perceive to have higher societal status than their male partner perceive him to be the weak one in the relationship and, as a result, report lower relationship satisfaction (Vink et al., 2021b). Also, men's feelings of masculinity were reduced when they interacted with a potential romantic female partner who outsmarted them because gender stereotypes describe men to be intelligent (Prentice and Carranza, 2002; Park et al., 2015). In a similar vein, men's implicit self-esteem suffers, and men are less optimistic about the future of their relationship when their female partner experiences a success that is more relevant to them (academic success vs. social success; Ratliff and Oishi, 2013). This evidence suggests that non-traditional couples are susceptible to stereotypical expectations in their environment and experience negative relationship outcomes due to these expectations.

Following these difficulties, it comes as no surprise that people prefer to avoid gender role violations (Amanatullah and Morris, 2010; Wallen et al., 2017). Moreover, in reaction to perceived gender role violations, people adhere even more to prescriptive gender stereotypes (Bosson et al., 2009; Willer et al., 2013; Cheryan et al., 2015). Men and women who try to break gender stereotypes thus face a vicious cycle. In order to deal with the difficulties that non-traditional couples experience, it seems more effective to understand and tackle gender stereotypes. This line of reasoning is in line with recent calls of researchers and practitioners to consider the broader system in dealing with gender stereotypes rather than focusing on the individual (Barker et al., 2010). The national culture is one of these larger systems that impact couples' decisions, behaviors, and feelings through its social policies and through the norms that are endorsed (e.g., Gerson, 1993; Ridgeway and Correll, 2000; Hook, 2006; Payne et al., 2017).

The Role of National Context

The gender-stereotypical culture of a country determines the extent to which a male breadwinner model is endorsed (Hook, 2006). It plays a crucial role in determining whether attitudes about status divisions within relationships will change (Gerson, 1993). In other words, the gender-stereotypical culture can make it easier or harder for men and women in non-traditional

couples to thrive in their relationships. When social policies of a country strongly endorse the male breadwinner model, it is economically less beneficial for couples to break with this model compared to countries that have moved away from the male breadwinner model (Hook, 2006). For example, the state's universal childcare is associated with women's full-time labor participation (Gornick et al., 1997). Also, Germany's social policies have long reinforced the male breadwinner model, whereas, in the United States, social policies less strongly endorse the male breadwinner model (Cooke, 2006). Subsequently, married men who do a larger share of the household work are more likely to divorce in Germany than married men in the United States (Cooke, 2006).

However, the decisions and behaviors of couples cannot be fully understood by economic and practical considerations. In countries that dissuade the male breadwinner norm, women still do most household and childcare-related tasks even if they earn more than their partner (Brines, 1994; Greenstein, 2000; Bittman et al., 2003). The gender-stereotypical culture influences the decisions and behaviors of non-traditional couples both *via* practical and economic considerations as well as *via* considerations of societal expectations (West and Zimmerman, 1987; Gerson, 1993; Hook, 2006). Societal expectations are reflected in country-level implicit gender stereotypes, which also affect the outcomes of people living in such countries (Greenwald et al., 2009; Nosek et al., 2009; Payne et al., 2017). To illustrate, in countries where people held stronger traditional gender associations, larger gender differences in math scores and achievement gaps between men and women in science were found (Nosek et al., 2009).

Following this line of reasoning, we will investigate how the national context affects non-traditional couples' outcomes by distinguishing two proxies for the gender-stereotypical culture in a country. That is the representation of women in non-stereotypical positions (characterized by the United Nations' Gender Empowerment Measure, GEM index) and the endorsement of implicit gender stereotypes (characterized by countries' average scores on the Gender-Career Implicit Association Task, IAT; Greenwald et al., 1998). The country's representation of women in counter stereotypical positions and its average implicit gender stereotypes define the lives of its inhabitants because they impact the rational and practical decision that couples make (e.g., what status division within the relationship is economically most beneficial?) Furthermore, the representation and salience of implicit gender stereotypes also impact the extent to which couples (unconsciously) anticipate negative social evaluations when they violate traditional gender norms. By including women's representation in senior positions as well as average country scores on the gender-career implicit association task, we can investigate how these two relevant proxies for the gender-stereotypical culture of a country influence relationship dynamics of men and women in non-traditional relationships. Following Hook (2006), we expect that both women's representation and average implicit gender associations will affect non-traditional couples in a similar (but not identical) way. By combining these two proxies for a country's gender-stereotypical culture, we aim to explain a significant amount of variance in non-traditional couples' experiences in different countries.

Overview of Study

In the current study, we will investigate how a country's gender-stereotypical culture affects men and women's relationship quality, satisfaction with their combination of work and family duties, experienced time pressure, and negative emotions. Relationship quality is an essential predictor of couples' commitment to their relationship, which predicts the relationship's persistence (Rusbult et al., 1998). Previous work has shown that women in non-traditional relationships experience decreased work-life satisfaction, more work-life conflict, and emotions such as guilt compared to women in traditional relationships (Vink et al., 2021a). By including work-life satisfaction, experienced time pressure, and negative emotions in this study, we can investigate how having a non-traditional relationship is related to these more individual life outcomes of both men and women. Furthermore, rather than including one objective indicator of the non-traditionality of a relationship, we will include three objective indicators: women's relative income, educational degree, and working hours in relation to her male partner. Previous work has established that status asymmetry can have negative consequences, now we can establish which indicator is leading.

We will operationalize a country's gender-stereotypical culture by including an indicator of the endorsement of traditional norms by inhabitants of a country (i.e., the average score on Implicit Association Task per country; IAT-score) as well as an indicator of real gender equality outcomes (i.e., women's representation in senior positions; GEM index). The IAT is a measure most often used in psychological research, whereas the GEM is often used in sociological research. Using both measures as indicators of a country's gender-stereotypical culture provides a unique way to combine psychological and sociological measures.

Hypotheses

In the present research, we will examine whether men and women in non-traditional relationships experience lower relationship and life outcomes than men and women in more traditional relationships. Furthermore, we will study whether the negative outcomes of being in a non-traditional relationship are qualified by gender empowerment and the endorsement of implicit gender stereotypes in the country that men and women live in. Specifically, we will test two pre-registered hypotheses:

H1: The higher women's status relative to their male partner (i.e., the higher women's relative income, educational degree, and working hours relative to their partner), the more negative relationship- and life-outcomes men and women report.

H2: Men and women in relationships in which women have higher status relative to their male partners who live in a country with less gender empowerment and more traditional implicit gender stereotypes will experience

worse outcomes compared to men and women in relationships in which women have higher status relative to their male partners and who live in a gender-egalitarian country.

MATERIALS AND METHODS

Participants and Design

To test our hypotheses, we used the European Sustainable Workforce Survey (ESWS; Van der Lippe et al., 2016). The ESWS is a multi-actor organizational survey conducted among employees in nine different countries; Bulgaria, Finland, Germany, Hungary, Netherlands, Portugal, Spain, Sweden, and United Kingdom. The ESWS data is collected in compliance with national, EU, and international ethics-related rules and professional codes of conduct. It has been reviewed by the second author's Faculty's Advisory Committee on Ethical Issues, which declared that no ethical approval is necessary. We excluded participants who were not in heterosexual relationships or whose own gender or their partner's gender was unknown. We excluded participants of whom we were unable to measure their relative income in relation to their total household income from our analyses. These were participants who did not fill out their income or participants of whom we were unable to measure their relative income (e.g., because their own income was higher than the end of the scale of the relative income measure).

Participants (N = 2,748 of which 42% men and 58% women; M_{age} = 45.03, SD_{age} = 10.78) were working in 113 different organizations and had completed a second stage of tertiary education (MA or MSC; 22.2%), upper secondary education (18%) or first stage of tertiary education (BA or BSC; 13.3%). Most participants were married to their partner (71%) and had children living at home (58.7%). Lastly, 12.9% of participants reported being divorced or separated before (see **Table 1** for the division of traditional vs. non-traditional couples across countries).

Procedure

Concerning the ESWS, participants (employees, managers, and the HR manager) were asked to fill out an online or paper-and-pencil questionnaire at their work after the organizations (often HR directors) agreed to participate. The survey took about 20 min to complete. For the current research, we mainly used employee data. The response rate of employees was, on average, 61% (Van der Lippe et al., 2016).

Materials

Demographic Background Information

Participants were asked to indicate their gender, age, marital status (i.e., married vs. cohabiting), whether they were divorced or separated before, and if they had children living at home.

Relative Income

To calculate women's income relative to their male partners, we used participants' net income in relation to their estimation

TABLE 1 | Participant characteristics.

		Total sample%	Male ppn%	Female ppn%	United Kingdom ppn%	German ppn%	Finnish ppn%	Swedish ppn%	Dutch ppn%	Portuguese ppn%	Spanish ppn%	Hungarian ppn%	Bulgarian ppn%
Relative income	Woman earns more	40.7	16.4	58.5	34.3	32.8	24.3	36.3	23.4	31.2	44.1	44.4	56.9
	Woman and man equal	2.7	2.0	3.1	1.9	3.3	10.0	2.8	3.2	1.8	0.0	1.5	2.7
	Man earns more	56.6	81.6	38.4	63.8	63.9	65.7	60.9	73.4	67.0	55.9	54.1	40.4
	N	2241	946	1295	105	119	70	220	458	115	118	357	679
Relative education	Woman more highly educated	35.9	28.4	40.6	35.9	23.1	31.9	38.7	29.0	36.3	40.9	38.0	39.3
	Both equally high educated	41.3	42.2	40.7	38.5	47.0	41.7	40.3	44.1	33.3	32.1	39.4	43.1
	Man more highly educated	28.8	28.4	18.7	25.6	29.9	26.4	21.0	26.9	30.4	27.0	22.6	17.6
	N	2689	1137	1552	117	134	72	238	501	138	137	452	900
Relative working hours	Woman works more hours	12.4	14.4	10.6	21.2	12.2	18.6	10	8.1	18.1	27.8	10.2	11.5
	Both work equal # of hours	48.7	45.7	51.2	25.3	24.2	32.6	54.7	17.5	51.4	21.1	68.5	70.3
	Man works more hours	38.9	39.9	38.2	53.5	63.6	48.8	35.3	74.7	30.5	51.1	21.3	18.1
	N	1890	838	1052	99	99	43	190	383	105	90	305	576

of their total household income. Net income was asked with the following question: "What are your net monthly earnings from your main job at this organization? Please refer to your average earnings in recent months." It was explained that net income refers to what participants have left every month after deducting national and local taxes and compulsory national insurance contributions. If participants did not fill out their net income in absolute numbers, they were asked to approximate their net income in 21 categories. These categories were based on a distribution of average income in participants' own country. To illustrate, Netherlands is a country with a higher average income than Spain. For this reason, the lowest category for participants from Netherlands included all net incomes below 820 euros, whereas this category for Spain included all net incomes below 260 euros. Similarly, the highest category for participants from Netherlands included all incomes above 3,290 euros, whereas this was 2,570 euros for Spanish participants.

Furthermore, participants were asked to indicate their total household income with the following question: "If you combine income from all sources and all household members, which category best describes your household's total net monthly income?" Participants could choose one of ten categories based on the average household net income per country. We combined participants' net income with the calculated categories and divided their total household income from participants' net income per country. To calculate participants' relative income for each country, we used each category's means and recoded every answer accordingly. We repeated this procedure for each country and then combined the nine different variables. Lastly, we detracted men's relative income in relation to their total household income from 1. Thus, our final relative income variable indicated the percentage of women's net income of the total household income.

Relative Education

To calculate women's educational degrees relative to their male partner's educational degree, we detracted the man's highest completed education from the woman's highest completed education. Participants' own and their partner's educational level were asked with one question: "What is the highest level of education that you/your partner have/has completed?" Answers ranged from 0 (*Not completed primary education*) to 7 (*Doctoral degree, Ph.D.*). Higher scores on the relative education variable thus indicate that the woman is higher educated than the man in the relationship.

Relative Working Hours

To calculate women's working hours relative to their male partner's working hours, we detracted the man's working hours from the woman's working hours. We used participants' and their partners' contracted working hours, which was asked with one question: "How many hours a week are you/is your partner contracted to work? Exclude any paid or unpaid overtime." We excluded answers above 80 h a week from our analyses due to plausibility concerns. Higher scores on the relative working hours variable thus indicate that the woman is working more hours than her male partner.

We decided to include relative *contracted* working hours of participants rather than *actual* working hours because the dataset only contains *actual* working hours of the participants themselves and not for their partners. However, the correlation between contracted working hours and actual working hours for participants themselves was very high ($r = 0.73$, $p < 0.001$).

Countries' Gender-Stereotypical Culture: Implicit Gender Stereotypes

To assess countries' implicit gender stereotypes, we used data made available by Project Implicit[1] (Greenwald et al., 1998; Nosek et al., 2009). Data were collected among visitors of the Project Implicit website who received educational feedback on social attitudes and stereotypes after participating in an Implicit Association Task. We used the Gender-Career IAT data between 2014 and 2018 and selected scores of participants living in one of the nine countries included in the ESWS (data available[2]). The Gender-Career IAT measures respondents' association strength of the groups: *men* (e.g., Paul, John) and *women* (e.g., Emily, Anna) with the concepts: *career* (e.g., career, salary) and *family* (e.g., home, children). The IAT consists of two compatible blocks, where respondents were to link the career-words to the male names and family-words to the female names, and two incompatible blocks, where respondents were to link the career-words to the female names and the family-words to the male names. The two compatible and two incompatible blocks were counterbalanced. There were three practice trials. D-scores were calculated by subtracting response latencies of incompatible blocks from compatible blocks and dividing the mean differences in latencies by respondents' standard deviation on all trials except for the three practice trials. This way, higher scores reflect more traditional implicit associations, and scores close to zero reflect

[1]https://implicit.harvard.edu

[2]https://osf.io/y9hiq/

TABLE 2 | Average D-scores of Gender-Career IAT from 2014–2018, GEM index and combined Z-scores of IAT and GEM (gender-stereotypical culture) for countries included in ESWS.

	Gender-stereotypical culture	IAT D-Score	GEM index
Sweden	1.62	0.322	0.883
Finland	1.29	0.334	0.853
Spain	1.01	0.332	0.776
United Kingdom	0.49	0.357	0.755
Portugal	0.39	0.346	0.681
Germany	0.27	0.384	0.816
Netherlands	0.15	0.397	0.844
Bulgaria	−0.27	0.364	0.595
Hungary	−1.29	0.414	0.560

Countries below the dotted line were considered traditional countries, and countries above the dotted line were considered egalitarian countries based on the combined z-scores.

more egalitarian implicit associations (Greenwald et al., 1998). Average D-Scores per country are shown in **Table 2**.

Countries' Gender-Stereotypical Culture: Gender Empowerment

In order to assess countries' gender empowerment, we used United Nation's Gender Empowerment Measurement (GEM) index, which is based on four measures: (1) women's share of legislators in the national parliament, (2) the percentage of female managers, legislators, and senior officials, (3) amount of female employees in professions and (4) the female-to-male wage ratio among full-time employees. The GEM index is argued to measure women's agency in society and control over political and economic resources (Maume et al., 2018). We used GEM scores as reported by Maume et al. (2018). The GEM ranges from 0 to 1, with higher scores indicating more gender egalitarianism (see **Table 2**).

Countries' Gender-Stereotypical Culture: Combined Measure

In order to create one variable of countries' gender-stereotypical culture, we calculated the average z-score of countries' implicit gender stereotypes and gender empowerment scores (see **Table 2**). Higher z-scores indicate a more egalitarian gender-stereotypical culture. Based on these scores, Sweden, Finland, Spain, the United Kingdom, and Portugal were classified as egalitarian countries. Germany, Netherlands, Hungary, and Bulgaria were classified as traditional countries (see **Table 2**).

Relationship Quality

Relationship quality was measured with one question of the time competition survey (Van der Lippe and Glebbeek, 2003). This question was; "In general, how satisfied are you with your relationship?" Answers ranged from 1 (*very unsatisfied*) to 10 (*very satisfied*). Relationship quality is a construct that is often measured with a single item (see, e.g., Hardie et al., 2014; Blom and Hewitt, 2019).

Work-Life Satisfaction

Work-life satisfaction was measured with one question: "How satisfied are you with the time you spend on paid work vs. the time you spend on other parts of your life?" (Van der Lippe et al., 2016). Answers ranged from 1 (*extremely dissatisfied*) to 10 (*extremely satisfied*).

Time Pressure

In order to measure time pressure, participants were asked to indicate how often the following happened to them: "I am under time pressure," "I wish I had more time for myself," "I feel I am under time pressure from others," and "I cannot deal with important things properly due to a lack of time" ($\alpha = 0.85$; Van der Lippe et al., 2016). Answers ranged from 1 (*always*) to 5 (*seldom*). We recoded scores so that higher scores indicate more time pressure.

Negative Emotions

In order to measure negative emotions, participants were asked to indicate how often during the past week: "you felt depressed," "you felt that everything you did was an effort," "your sleep was restless," "you were happy (recoded)," "you felt lonely," and "you felt sad" ($\alpha = 0.80$; Van der Lippe et al., 2016). Answers ranged from 1 (*never*) to 5 (*all the time*).

RESULTS

Preliminary Analyses

First, we conducted a correlational analysis to investigate whether background variables were associated with our independent and dependent variables (see **Table 3**). Participants' age, marital status, and whether they had children living at home were all associated with several outcome variables. For instance, older participants reported lower relationship quality but higher work-life satisfaction. We included these variables as covariates in our multilevel models. Furthermore, we included participants' total household income as another covariate to our models. We did this to show that the effects of income, education, and working hours are indeed due to women's relative position compared to her partner and not because of absolute differences (e.g., couples with higher income in general compared to couples with lower income).

Next, to prevent multicollinearity, we compared the correlations of our three independent (i.e., relative income, education, and working hours) and moderating variables (i.e., countries' gender empowerment and implicit gender stereotypes; see **Table 3**). None of the correlations between the three independent variables were higher than $r = 0.50$ (which we considered problematic regarding multicollinearity). We aim to investigate whether one of the three objective statuses plays a crucial role in couples' relationship and life outcomes. For this reason, we prefer to use them as separate variables in our model. However, the correlation between the dummies of gender empowerment and implicit gender stereotypes was $\varphi = 0.43$, $p < 0.001$. We aim to show how gender stereotypes in countries contribute to couples' relationship and life outcomes. For this reason, we decided to create z-scores out of the IAT scores and GEM index per country and calculate the mean between these two z-scores. Based on this mean, we created a dummy variable of traditional countries vs. egalitarian countries (see **Table 3**). We considered combining the two indicators more optimal than running two separate models as this way we were able to run fewer analyses, preventing multiple comparisons. However, we conducted separate analyses for both indicators of a countries' gender-stereotypical culture, which did not result in many different patterns in the reported results. The only difference we found was that the interaction of relative education and culture on relationship quality was driven by implicit gender stereotypes per country and not by the gender empowerment index.

Overview of Multilevel Analyses

We conducted two-level multilevel random intercept regression models in SPSS. All models included organization as a Level 2 variable as participants work in 259 different organizations (i.e., multilevel data). First, we conducted multilevel regression

TABLE 3 | Correlation analyses of background, independent, and dependent variables.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. Age	–																					
2. Age partner	0.86**	–																				
3. Gender	−0.07**	0.17**	–																			
4. Marital status	0.32**	0.31**	−0.03	–																		
5. Divorced before	0.13**	0.07**	−0.03	−0.27**	–																	
6. Children living at home	0.10**	0.12**	0.04	−0.20**	0.05*	–																
7. Own education level	−0.14**	−0.11**	0.15**	−0.02	−0.08**	−0.01	–															
8. Partner's education level	−0.12**	−0.13**	−0.02	−0.02	−0.04	−0.03	0.59**	–														
9. Working hours	−0.06**	−0.10**	−0.18**	−0.05*	0.04	0.02	−0.03	0.00	–													
10. Partner's working hours	−0.06*	−0.01	0.22**	−0.05*	0.04	0.09**	0.01	0.02	0.25**	–												
11. Net income	0.06*	0.04	−0.04	0.01	0.03	0.02	−0.06**	−0.04	0.15**	0.14**	–											
12. Total household income	−0.04	−0.05**	−0.05**	0.06**	0.01	−0.07**	0.31**	0.36**	0.07**	0.05*	0.19**	–										
13. Relative income	−0.01	0.11**	0.49**	−0.06**	0.02	0.06**	0.17**	0.07**	0.01	0.17**	0.01	−0.03	–									
14. Relative education	−0.08**	−0.05*	0.13**	−0.01	−0.02	−0.01	0.03	−0.14**	0.03	0.09**	0.01	−0.02	0.22**	–								
15. Relative working hours	0.01	0.01	0.04	−0.04	0.02	0.12**	0.08**	0.10**	0.12**	0.09**	0.10**	0.06*	0.23**	0.05*	–							
16. Countries' IAT-score	−0.02	−0.02	0.00	−0.03	−0.02	0.05**	−0.09**	−0.03	−0.03	−0.06**	0.53**	0.05**	−0.04	−0.04*	−0.12**	–						
17. Countries' GEM-index	−0.02	−0.06**	−0.18**	−0.02	0.04*	−0.04	0.00	0.06**	−0.08**	−0.21**	−0.44**	0.18**	−0.18**	−0.09**	−0.23**	−0.30**	–					
18. Culture (combined z-scores IAT and GEM)	0.00	−0.03	−0.11**	0.01	0.03	−0.06**	0.05**	0.05**	−0.03	−0.09**	−0.59**	0.08**	−0.09**	−0.03	−0.06**	−0.81**	0.81**	–				
19. Relationship quality	−0.09**	−0.11**	−0.08**	0.02	−0.03	0.05*	−0.02	0.03	−0.01	−0.02	0.04	0.05*	−0.10**	−0.01	−0.01	0.03	0.04	0.01	–			
20. Work-life satisfaction	0.09**	0.06**	−0.03	0.09**	−0.03	−0.04*	−0.05*	−0.06**	−0.09**	−0.03	0.03	0.03	−0.06**	−0.05*	−0.04	0.04	0.06**	0.01	0.15**	–		
21. Time pressure	0.00	0.00	0.00	0.02	−0.01	0.02	−0.02	−0.01	−0.03	−0.01	−0.04	−0.02	0.00	0.03	−0.01	−0.01	0.05*	0.04	0.04*	0.05**	–	
22. Negative emotions	0.04	0.08**	0.15**	0.00	−0.01	0.00	0.01	−0.04*	−0.02	0.07**	−0.10**	−0.19**	0.12**	0.05**	0.06**	−0.14**	−0.18**	−0.02	−0.31**	−0.25**	−0.08**	–

$^{**}p < 0.01$ and $^{*}p < 0.05$.

Gender is dummy-coded with 1 = male and 2 = female; Marital status is dummy-coded with 0 = cohabiting and 1 = married; Children living at home is dummy-coded with 0 = yes and 1 = no.

Relative income is the percentage of the woman's income of the total household income.

Relative education is calculated by subtracting the man's educational level from the educational level of the woman.

A similar calculation was conducted for relative working hours.

Higher scores thus always indicate a higher relative status of the woman in relation to her male partner.

models without any predictors to justify the need for random intercept models. These models indicated that there is an especially high variance on the organization level for work-life satisfaction (25.2%), but also relationship quality (5.2%) and negative emotions (5.0%).

In Model 1, we included background variables (i.e., age, marital status, children living at home, and total household income) and women's income, education, and working hours relative to their partners. In Model 2, we ran one model with the main effects of countries' gender-stereotypical culture (mean z-scores of IAT and GEM). In Model 3, we ran one model which added the interaction effects of women's relative status (income, education, and working hours) and countries' gender-stereotypical culture (see **Supplementary Appendix A** for regression coefficients and standard errors of all models). Furthermore, in the case of significant interactions, the full model is analyzed separately for traditional vs. egalitarian countries. In case of significant interactions, we will report the simple slopes for the significant status indicators (M-1SD and M + 1SD). Lastly, the ESWS (Van der Lippe et al., 2016) only includes nine different countries, so it could be that our results are driven by one very influential country. In order to check for influential countries, we conducted nine similar analyses, excluding every country once (the Jackknife procedure; Rodgers, 1999; see **Supplementary Appendix B**). Furthermore, we tested whether participants' gender qualified our hypotheses. We reran all models and started with a model that included the main effects of participants' gender (Model 1). Then, we ran an extra model in which we investigated interaction effects of participants' gender and the relative status indicators (Model 2), and a model that additionally included all two-way interactions of relative status and culture. Last, we ran a model that tested for a three-way interaction between gender, culture, and the relative status indicators (see **Supplementary Appendix C**). The reported effects below were not qualified by participants' gender. However, we found three additional effects of participants' gender, which we have summarized and shown in the **Supplementary Appendix C**.

Does Women's Higher Relative Status Predict Negative Relationship and Life Outcomes?

In line with Hypothesis 1, participants in relationships in which the woman earns more than her male partner reported lower relationship quality and more negative emotions (see **Table 4**). Furthermore, participants in relationships in which the woman is higher educated than the man reported more time pressure (see **Table 4**). However, we found no support for Hypothesis 1 on some of the other variables. There were no associations of relative working hours on our dependent variables (see **Table 4**). Women's status relative to their partner was not associated with work-life satisfaction (see **Table 4**). Also, relative income was not associated with experienced time pressure, and relative education was not associated with relationship quality and negative emotions (see **Table 4**).

Does Countries' Gender-Stereotypical Culture Qualify These Results?

In line with Hypothesis 2, we found a significant interaction effect of women's relative income and countries' gender-stereotypical culture on participants' relationship quality (see **Table 4**). Running the models separately for traditional and egalitarian countries, we found that participants living in traditional countries reported lower relationship quality when they had a relationship in which the woman earns more than her male partner, $b = -1.30$, $SE = 0.31$, $p < 0.001$. This was not the case for participants living in egalitarian countries, $b = 0.22$, $SE = 0.63$, $p = 0.722$. Simple slope analyses showed a marginally significant effect for couples in which the woman earns more than the man, $b = -0.31$, $SE = 0.19$, $p = 0.097$. For these couples, living in a traditional country was associated with lower relationship quality than living in an egalitarian country. Simple slope analyses showed no significant effects for couples in which the man earns more than the woman, $b = 0.29$, $SE = 0.17$, $p = 0.101$. In sum, these analyses show that men's and women's relationship quality suffers when the woman earns more than her male partner, but this is only the case when these men and women live in a country where a traditional gender-stereotypical culture is endorsed.

Furthermore, we found a significant interaction effect of women's relative education level and countries' gender-stereotypical culture on relationship quality (see **Table 4**). We found no association of women's educational level relative to her partner and participants' relationship quality in traditional countries, $b = -0.04$, $SE = 0.04$, $p = 0.325$. In contrast, in egalitarian countries, participants reported higher relationship quality when they were in a relationship in which the woman is higher educated than the man, $b = 0.14$, $SE = 0.06$, $p = 0.025$. Simple slope analyses showed a marginally significant effect for couples in which the woman is higher educated than the man, $b = -0.26$, $SE = 0.15$, $p = 0.091$. For these couples, living in an egalitarian country is associated with higher relationship quality compared to living in a traditional country. Simple slope analyses showed no effects for couples in which the man is higher educated than the woman, $b = 0.15$, $SE = 0.18$, $p = 0.414$.

We also found a significant interaction effect of women's relative working hours and countries' gender-stereotypical culture on work-life satisfaction (see **Table 4**). However, we found no significant differences of participants living in traditional, $b = -0.01$, $SE = 0.01$, $p = 0.188$, vs. egalitarian countries, $b = 0.02$, $SE = 0.01$, $p = 0.105$. Simple slope analyses showed that participants in a relationship in which the man works more hours than the woman were more satisfied with how they combined work and private life, $b = 0.47$, $SE = 0.20$, $p = 0.022$. In contrast, there was no significant effect of participants in a relationship in which the woman works more hours than the man, $b = -0.10$, $SE = 0.20$, $p = 0.623$.

We also found a significant interaction effect of women's relative working hours and countries' gender-stereotypical culture on negative emotions (see **Table 4**). However, we found no significant differences of participants living in traditional, $b = 0.00$, $SE = 0.01$, $p = 0.246$, vs. egalitarian countries, $b = -0.01$, $SE = 0.00$, $p = 0.109$. Simple slope analyses showed

TABLE 4 | Hierarchical linear regression models of main effects of women's status relative to their partners on dependent variables (model 1) and of main and interaction effects of women's relative status and culture on dependent variables (model 3).

	Relationship quality		Work-life satisfaction		Time pressure		Negative emotions	
	b (SE)	*P*	*b (SE)*	*p*	*b (SE)*	*p*	*b (SE)*	*p*
Model 1								
Relative income	**−1.00 (0.28)**	**< 0.001**	−0.33 (0.29)	0.254	−0.01 (0.15)	0.926	**0.26 (0.09)**	**0.003**
Relative education	0.03 (0.03)	0.446	−0.04 (0.04)	0.281	**0.04 (0.02)**	**0.022**	0.00 (0.01)	0.767
Relative working hours	−0.00 (0.00)	0.950	−0.00 (0.01)	0.415	−0.00 (0.00)	0.227	0.00 (0.00)	0.577
Model 3								
Relative income	0.16 (0.62)	0.791	−0.28 (0.66)	0.674	0.06 (0.35)	0.870	**0.50 (0.20)**	**0.012**
Relative education	**0.15 (0.06)**	**0.019**	−0.01 (0.06)	0.878	0.06 (0.03)	0.074	−0.02 (0.02)	0.286
Relative working hours	−0.00 (0.01)	0.698	0.02 (0.01)	0.095	−0.00 (0.01)	0.655	−0.00 (0.00)	0.142
Countries' gender-stereotypical culture	−0.01 (0.11)	0.917	0.19 (0.16)	0.242	−0.07 (0.06)	0.242	−0.06 (0.05)	0.289
Relative income × culture	**−1.47 (0.69)**	**0.034**	−0.04 (0.73)	0.957	−0.08 (0.39)	0.844	−0.30 (0.23)	0.179
Relative education × culture	**−0.18 (0.07)**	**0.014**	−0.04 (0.08)	0.570	−0.03 (0.04)	0.507	0.03 (0.02)	0.149
Relative working hours × culture	0.01 (0.01)	0.631	**−0.03 (0.01)**	**0.020**	−0.00 (0.01)	0.842	**0.01 (0.00)**	**0.045**

Bold values represent significant effects.

that participants in a relationship in which the man works more hours than the woman experienced less negative emotions, $b = -0.13$, $SE = 0.07$, $p = 0.049$, whereas there was no significant effect of participants in a relationship in which the woman works more hours than the man, $b = 0.02$, $SE = 0.07$, $p = 0.793$.

We found no support for Hypothesis 2 on women's relative status (i.e., relative income, education, and working hours) and experienced time pressure and negative emotions (see **Table 4**).

Were There Influential Countries Driving These Results?

Effects remain quite similar when excluding every country once from the analyses (see **Supplementary Appendix B**). However, the effect of women's relative income on experienced negative emotions became non-significant when excluding Bulgaria. The effect of women's relative education on experienced time pressure became non-significant when excluding Bulgaria. The interaction of women's relative income and gender-stereotypical culture on relationship quality became marginally significant when excluding Sweden and non-significant when excluding Bulgaria. The significant interaction of women's relative working hours and gender-stereotypical culture on work-life satisfaction became marginally significant when excluding Sweden and Portugal (see **Supplementary Appendix B**). The results that change due to the jackknife procedure need to be interpreted with care.

DISCUSSION

In this paper, we investigated the role of national context on relationship and life outcomes of men and women in relationships in which the woman has surpassed the man in societal status. Furthermore, we investigated whether countries' gender-stereotypical culture (i.e., gender empowerment and implicit gender stereotypes) qualified men and women's relationship and life outcomes in non-traditional relationships. We replicate and extend previous work showing first evidence of the difficulties men and women experience when they are in a relationship in which the woman has higher status than the man. Our results suggest that especially women's income and -to a lesser extent- educational degree relative to their male partner negatively impair relationship and life outcomes. When men and women were in a relationship where the woman earns more than the man, they reported lower relationship quality and experienced more negative emotions. When men and women were in a relationship where the woman is higher educated than the man, they experienced more time pressure. Furthermore, these negative outcomes for non-traditional couples are qualified by the gender-stereotypical culture of a country. The salience of gender inequality in a country was conceptualized by a normative, more implicit indicator (i.e., inhabitants' average implicit gender stereotypes) and a more explicit indicator (i.e., women's representation in non-stereotypical roles) of a country's gender-stereotypical culture. This combination of traditional norms and real outcomes in countries affected the relationship quality of non-traditional couples. Specifically, men and women living in traditional countries reported lower relationship quality when they were in a relationship in which the woman earns more than her partner. On the other hand, participants living in egalitarian countries did not differ in relationship quality regardless of the woman's relative income. Furthermore, we found that men and women living in egalitarian countries reported higher relationship quality when they were in a relationship in which the woman is more highly educated than the man, whereas this was not the case for men and women living in traditional countries.

It is argued that it becomes more accepted for women to be educated and potentially even higher educated than their partner because these relationships are nowadays more common in most European countries (Schwartz and Han, 2014; De Hauw et al., 2017). For this reason, relationships in which the woman is more highly educated than the man have become more stable than before (Schwartz and Han, 2014). On the other hand, although

increasing in frequency, relationships in which the woman earns more than the man are still less common (Portegijs and Van den Brakel, 2018; Van Bavel et al., 2018). People still expect men to be breadwinners of their family, whereas they expect women to be their family's primary caregiver (Park et al., 2010; Morgenroth and Heilman, 2017). Rather than practical differences such as differences in working hours, it seems that especially symbolic status differences between couples explain negative outcomes for non-traditional couples. To this end, an increasing number of paid hours of women alone is not enough to change gender inequality; changing the culture in society is at least as necessary.

Limitations and Suggestions for Future Research

The national context seems to have a less direct impact on men and women's life outcomes (i.e., work-life satisfaction, experienced time pressure, and negative emotions). It could be that the gender-stereotypical culture of a country affects couples more indirectly. To illustrate, many women in Netherlands -a country in this study considered to have a traditional gender-stereotypical culture- work part-time (Portegijs and Van den Brakel, 2018). Dutch women who experienced negative life outcomes due to non-traditional divisions of paid work within their relationship might have already reduced their working hours to overcome these negative outcomes. Consequently, they no longer experience time pressure or work-life dissatisfaction because of violating traditional gender roles but have still adjusted their behavior to match the gender-stereotypical culture. Future longitudinal research is needed to investigate the indirect impact of a country's gender-stereotypical culture on the life outcomes of non-traditional couples.

A limitation of this research is that there were only nine countries in our dataset. Future research should replicate these effects by including more countries. Rather than including a normative (i.e., implicit gender stereotypes) and factual (i.e., gender empowerment) indicator of countries' gender-stereotypical culture, future research could investigate the role of a more explicit indicator: the salience of non-traditional relationships in a country. The frequency of non-traditional relationships within a country might also capture more indirect ways in which the gender-stereotypical culture affects non-traditional couples. The countries in which non-traditional couples are least common might also be the countries where many couples have internalized the gender-stereotypical culture and have adjusted their roles in the relationship to fit the male breadwinner model. Next to these country-level characteristics, it could be argued that individual- and community-level characteristics influence couples as well. For instance, women's own implicit gender stereotypes influence how they cope and behave when they perceive to have surpassed their partner in status (Vink et al., 2021a). Also, divorce rates of marriages in which women are higher educated than their male partners are lower in communities where they are more common than communities with more traditional marriages (Theunis et al., 2018). Based on this, a couple's social network (i.e., having many friends who are also in non-traditional relationships) or working in an organization in which many women have surpassed their partner in status might buffer the negative relationship outcomes for non-traditional couples. People unconsciously shape their implicit gender associations by seeing men and women in typical roles, and when many couples have atypical gender roles, stereotypical associations also become less traditional (Payne et al., 2017). Furthermore, friends and colleagues might provide social support, which is an important factor predicting individuals' well-being and outcomes. Therefore, social support might be a buffer for couples who break with traditional prescriptive gender stereotypes (Abendroth et al., 2012). Our results suggest that couples' decisions should not be seen as a private matter but are rather influenced by societal expectations and norms. Future research could include some of the abovementioned characteristics of the context to investigate how they interact and shape non-traditional couples' realities.

Some of our findings became less strong when one country was excluded from the analysis, indicating some influential countries in our dataset (Rodgers, 1999). Bulgaria was the most influential country and was also the country with the most traditional gender-stereotypical culture. It could be that the gender-stereotypical culture is most salient for non-traditional couples living in Bulgaria and thus also has the most substantial direct impact on the relationship and life outcomes of men and women. Future research should include more countries and investigate whether the salience of a countries' gender-stereotypical culture indeed explains these effects.

Lastly, women's relative societal status within the relationship did not affect how satisfied men and women were with their work-life combination. This finding contrasts with earlier findings showing that women reported lower work-life satisfaction in a diary setting when they perceived to have higher societal status than their partner (Vink et al., 2021a). General work-life satisfaction might be something different from daily work-life satisfaction. General measures often show less variety than daily measures (e.g., general measures are more susceptible to socially desirable responses than daily measures; Ohly et al., 2010). For this reason, it could be that the decreased daily work-life satisfaction that non-traditional couples experience is not reflected in their general work-life satisfaction. Non-traditional couples that have experienced dissatisfaction with their work-life combination for a more extended period might have already adjusted their behavior (e.g., by the woman reducing her work hours; Vink et al., 2021a).

Implications

This work shows how a countries' gender-stereotypical culture influences people's relationship and life outcomes and highlights the importance of a structural rather than an individual approach in tackling gender inequality for close relationships. The salience of traditional gender stereotypes prescribing men to be the breadwinner and women to be the primary caregiver of their family on a national scale influences the relationship quality of men and women who break with these expectations. Specifically, our work shows that men and women in relationships in which the woman earns more than her male partner experience more difficulties than couples in more traditional relationships.

Furthermore, this is especially the case in countries that endorse traditional gender attitudes (i.e., Hungary, Bulgaria, Netherlands, Germany) and have fewer women in senior positions (i.e., Portugal, Bulgaria, Hungary). Our findings have implications for evolutionary psychologists who argue that there are universal partner preferences between men and women, such that women in general desire partners with good providing skills, whereas men desire partners with good nurturing skills (e.g., Buss, 2011). Our findings show that these preferences may not be so universal and depend at least to some extent on the social norms and national culture, which is in line with scholars who show how partner preferences are influenced by the extent to which countries endorse gender-egalitarian cultures (Zentner and Eagly, 2015).

If social norms about who should be the breadwinner and who should be the caregiver change, couples in which the woman is the one with higher status in the relationship might experience fewer difficulties. For couples living in egalitarian countries, men and women reported higher relationship quality when they were in a relationship in which the woman is more highly educated than the man. This finding is in line with Schwartz and Han (2014). They state that because relationships in which women are more highly educated than their male partners have become more common, these relationships become more accepted and more stable (Schwartz and Han, 2014). The growing evidence that individual outcomes improve not only from interpersonal and more individual approaches (e.g., couple therapy) but also from structural change is essential information for governments and policymakers who try to improve gender equality within societies.

CONCLUSION

We show first evidence that countries' gender-stereotypical culture influences men and women in relationships in which the woman is the one with the highest status of both partners. It turns out to be a bottleneck when women earn more than their male partners and break with the male breadwinner model. These couples' difficulties are especially salient in countries that endorse the male breadwinner model and have a traditional gender-stereotypical culture. On the other hand, countries characterized by a more egalitarian gender-stereotypical culture seem to facilitate relationships in which men and women have equal status or women with higher status than their male partners.

AUTHOR'S NOTE

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DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: Data is stored at DANS (Data Archive and Networked Services of the Royal Netherlands Academy of Arts and Sciences) with "Restricted Access." This means that the data are protected and not directly accessible. However, other researchers can request permission to use the (anonymously) stored data. TL has to approve before access is given. Requests to access these datasets should be directed to TL, t.vanderlippe@uu.nl.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

MV, TL, and BD contributed to the conception of the study. MV and BD pre-registered the hypotheses and analyses. TL was responsible for data collection. MV organized the dataset and wrote the first draft of the manuscript. MV and TL performed the statistical analyses. TL, BD, and NE wrote sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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An intersectional lens on young leaders: bias toward young women and young men in leadership positions

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Research has recognized age biases against young leaders, yet understanding of how gender, the most frequently studied demographic leader characteristic, influences this bias remains limited. In this study, we examine the gender-specific age bias toward young female and young male leaders through an intersectional lens. By integrating intersectionality theory with insights on status beliefs associated with age and gender, we test whether young female and male leaders face an interactive rather than an additive form of bias. We conducted two preregistered experimental studies (N_1 = 918 and N_2 = 985), where participants evaluated leaders based on age, gender, or a combination of both. Our analysis reveals a negative age bias in leader status ascriptions toward young leaders compared to middle-aged and older leaders. This bias persists when gender information is added, as demonstrated in both intersectional categories of young female and young male leaders. This bias pattern does not extend to middle-aged or older female and male leaders, thereby supporting the age bias against young leaders specifically. Interestingly, we also examined whether social dominance orientation strengthens the bias against young (male) leaders, but our results (reported in the SOM) are not as hypothesized. In sum, our results emphasize the importance of young age as a crucial demographic characteristic in leadership perceptions that can even overshadow the role of gender.

KEYWORDS

leadership, young age, gender, status, intersectionality, ageism, social dominance orientation

1. Introduction

As the workforce diversifies in age and young-led tech industries continue to expand their influence on the economy, an increasing number of skilled young professionals are stepping into leadership positions. In fact, 38% of American workers now report to a young leader (Kaufman, 2017). Consequently, examining how young leaders are perceived has become increasingly important for organizational scholars.

Research has identified negative perception biases against young adults in leadership positions (e.g., Buengeler et al., 2016; Kunze and Menges, 2016). This is consistent with studies on gender and leadership, which reveal similar biases against female leaders (Ridgeway, 2001; Eagly and Karau, 2002; Rudman et al., 2012). These biases can be explained,

in part, by the lower status beliefs associated with demographic characteristics such as young age or gender (i.e., diffuse status characteristics, e.g., Lianidou and Zheng, 2022). Status beliefs can be defined as "widely held cultural beliefs that associate greater social significance and general competence […] with one category of a social distinction over another" (Ridgeway, 2001, p. 638). However, our understanding of the status beliefs associated with the intersections of demographic characteristics, such as age *and* gender, is still limited.

To thoroughly examine the age bias toward young leaders, it is crucial to adopt an *intersectional lens*, especially considering the well-documented bias women face in leadership positions (e.g., Koenig et al., 2011). Intersectionality offers a framework for investigating how multiple aspects of an individual's identity, such as age and gender, intersect and influence their experiences and challenges (Crenshaw, 1990; Cole, 2009). However, the nature of intersectional bias toward young women and men in leadership is not understood yet. When people apply an intersectional lens, do young female leaders face bias due to their young age *and* female gender added together, resulting in a "double jeopardy" effect (additive effect; e.g., Berdahl and Moore, 2006; Nelson, 2016)? Or do they face bias based on only one (or neither) of these factors, resulting in an "intersectional escape" (interactive effect; e.g., Purdie-Vaughns and Eibach, 2008; Martin et al., 2019)? Similarly, does the gender of young male leaders counterbalance a potential age bias (i.e., additive effect), or is bias still present as it may primarily be due to their young age (i.e., interactive effect)?

In this study, we take an intersectional approach to examine age bias in people's perceptions of leader status—including respect, prominence, and prestige (e.g., Djurdjevic et al., 2017). To do so, we develop theory on biases against young female and male leaders integrating status characteristics reasoning (status characteristics theory; Berger et al., 1977; Ridgeway et al., 1985) with intersectionality theory and research (Hall et al., 2019; Petsko et al., 2022). To predict the intersectional bias, we further theorize on group prototypicality concerning age and gender for young women and men. Group prototypicality helps to explain why certain group members are considered more representative of a specific group than others (Purdie-Vaughns and Eibach, 2008; Hall et al., 2019). Comparing people's leader status perceptions as seen through different lenses—age (i.e., young leaders), gender (i.e., female and male leaders), and age *and* gender (i.e., young female and male leaders)—allows us to determine the nature of the intersectional bias toward young female and male leaders.

With our research, we offer two important contributions to research on age bias in leadership. First, we extend the growing literature on intersectionality in leadership research (e.g., Rosette et al., 2016, 2018) to age and gender, exploring how these factors may influence the perceptions of leaders. By comparing the intersection of age with gender to both single group categories, we can determine which aspect carries greater influence in evaluations of young female and young male leaders. Second, we deepen understanding of age bias toward young adults in leader roles from a status characteristics perspective and reveal lower leader status as a critical correlate. Through empirical evidence from two pre-registered experimental studies ($N_1 = 918$ and $N_2 = 985$), we reveal the relative importance of young age as a key demographic characteristic, surpassing gender, the most studied demographic leader characteristic (Lianidou and Zheng, 2022).

2. An intersectional lens on young leaders

In psychological and management science, *intersectionality* (Crenshaw, 1990; Cole, 2009) refers to how biases and stereotypes manifest simultaneously across multiple group categories, such as race, gender, or age (e.g., Rosette et al., 2018). When group categories, like age or gender, intersect, they can form a new category with unique biases and stereotypes that may be separate from the original group categories.

The lens-based perspective of intersectional stereotyping (Petsko et al., 2022) suggests that people use separate lenses, such as gender, age, or intersectionality, to perceive and categorize others. Importantly, according to this model, only one lens is used at a time during perception and stereotyping. The choice of lens depends on factors like *accessibility* (how easily it can be retrieved from memory), *fit* (how well it aligns with the specific context), *distinctiveness* (how noticeable the group category is), and the individual's *goal* (their motivation to categorize based on one group category over another; Petsko and Bodenhausen, 2020; Petsko et al., 2022).

In general, people do not use an intersectional, age, or gender lens by default (Petsko et al., 2022). Instead, they may opt for the most accessible, salient, and contextually fitting lens. When evaluating young female and young male leaders, individuals may apply lenses based on age, gender, or their intersection. People may perceive young female leaders through a gender lens, categorizing them as *women*, or through an age lens, categorizing them as *young individuals*. Alternatively, people may apply an intersectional lens, categorizing young female leaders as *young women*.

The lens people adopt to perceive leaders may have consequences, as each lens emphasizes specific attributes and *status ascriptions* tied to a particular group (Petsko et al., 2022). Unlike specific status, which arises from well-defined attributes directly related to ability, education, or functional background, *ascribed* status is based on diffuse characteristics like gender or age (e.g., Lianidou and Zheng, 2022). Indeed, status characteristics theory posits that people ascribe higher status to certain social groups (e.g., men, older adults) and lower status to others (e.g., women, young adults; Berger et al., 1977; Ridgeway et al., 1985). As ascribed status is independent of an individual's skills and expertise, it can lead to *biased* expectations and decisions regarding leaders.

Both gender and age bias involve one group being associated with greater social significance, competence, and status than others. Men, who tend to hold dominant positions in society, are typically seen as the gender-neutral standard, whereas women are viewed as more gender-specific (Bailey et al., 2019). Dominant positions afford men more access to power and resources than women, leading to greater respect and prestige (Ridgeway, 1991). Regarding age, research indicates that older adults usually possess more social power and status than young adults (e.g., Sidanius and Pratto, 1999; Triana et al., 2017). Consequently, there is an unequal distribution of social status among gender and age groups, with men and older adults generally having higher status than women and young adults.

The primary difference between gender and age bias lies in the roots of their respective status characteristics (Martin and North, 2022). Gender is perceived as a more static status characteristic, with the categories of men, women (and nonbinary individuals).[1] In contrast to gender, age is a more dynamic and continuous status characteristic. Age-based status ascriptions—both positive and negative—are relevant for all individuals over time, assuming they experience a sufficient lifespan. Due to age's dynamic nature and the natural aging process, age bias is often less acknowledged or more accepted than gender bias (Nelson, 2016; Martin and North, 2022). Individuals may believe that young adults aspiring to or holding leadership positions should "wait their turn," and perceive it as fair that young adults do not hold leadership positions. We therefore argue that young age is even more problematic than gender regarding biases in leader status perceptions. In the following sections, we will theorize on the intersection of age and gender in relation to leader evaluations based on their respective group prototypicality.

2.1. Bias toward young female leaders

Group prototypicality, referring to the extent to which an individual is perceived as a typical or representative member of a specific social group (e.g., Rosch and Mervis, 1975; Rosch, 1978), plays a crucial role in leader evaluations. More visible, and easily categorized, prototypical members can face an amplified bias, whereas less prototypical members may experience a diluted bias (Hall et al., 2019). Leaders' prototypicality in terms of age and gender may thus shape an intersectional bias toward young female leaders.

We suggest that within their gender group, young women are perceived as more prototypical of the category "women" than older women. Stereotypes associated with women (e.g., femininity) may align more closely with stereotypes associated with young age (e.g., attractiveness, vitality) than older age (e.g., decreased attractiveness; Kite et al., 2005). This greater congruence between stereotypes of women and those of a young age makes young women more salient and representative of their gender group compared to older women (Hall et al., 2019). Consequently, young women may be perceived as prototypical for the category of women, while older women are seen as less prototypical, thereby diluting gender-based status ascriptions for older women (i.e., intersectional escape; Martin et al., 2019).

However, we assume that within the young age group, women are perceived as less prototypical of the category "young adults" compared to men. Specifically, the gender-based social hierarchy (Ridgeway, 1991) may cause people to view young women as less representative members of the younger age group compared to young men. This perception arises because men, due to their dominant societal position, form the gender-neutral standard, while women are seen as more gender-specific (e.g., Bailey et al., 2019). Moreover, stereotypes associated with younger age (e.g., self-confident, assertive; Kite et al., 2005) may align more closely with stereotypes linked to men (i.e., agentic, assertive) than with those connected to women (i.e., communal attributes, e.g., Eagly et al., 2020). As a result, young men are highly prototypical for the young age group, amplifying age status ascriptions. In contrast, young women's less prototypical status may dilute age-based status ascriptions.

Building on young women's gender prototypicality, we anticipate that young female leaders will encounter a non-additive, interactive form of bias. We propose that young female leaders face relatively more gender-based than age-based status ascriptions. Although both gender and age are likely to contribute negatively to leader status ascriptions, we posit that young age outweighs gender in terms of its impact on status ascriptions. This is due to the dynamic and continuous nature of age as a status characteristic, compared to the more static nature of gender as a status characteristic (e.g., Martin and North, 2022). In other words, for women leaders we propose that it is more detrimental to be perceived as young rather than as a young female (i.e., due to diluted status ascriptions for young female leaders), whereas being seen as a female leader should yield less negative perceptions than being perceived as a young leader (as being young is more problematic than being female). Consequently, we hypothesize that "young leaders" (i.e., being viewed through an age lens only) receive more negative status ascriptions than "young female leaders" (i.e., being viewed through an intersectional lens; *H1a*). Additionally, the categorization as "young female leaders" might be assessed more negatively than "female leaders" (i.e., being viewed through a gender lens only; *H1b*) due to (diluted) age-based status ascriptions for young female leaders. We hypothesize:

> *H1a/b: Young female leaders are assigned (a) higher leadership status than young leaders in general but (b) lower leadership status than female leaders in general.*[2]

2.2. Bias toward young male leaders

So far, our theorizing has centered on the intersectional bias toward young female leaders. However, we argue that there may also be bias against young male leaders, manifested in diminished perceptions of their leader status. We propose that this bias could emerge not only when people evaluate young male leaders through an age lens (i.e., as young adults) but also when applying an intersectional lens (i.e., as young men).

We suggest that within their gender group, young men are perceived as more prototypical of the category "men" than older men. Stereotypes associated with men (i.e., agentic, assertive, e.g., Eagly et al., 2020) more closely align with stereotypes associated with younger individuals (e.g., self-confident, assertive) than those related to older individuals (i.e., being less agentic, e.g., Kite et al., 2005). Consequently, the gender prototypicality of young men stems from a greater overlap

1 In line with the gender-based hierarchy (Berger et al., 1977; Ridgeway, 2001) and the "men as the standard-paradigm" (e.g., Bailey et al., 2019), status ascriptions based on gender should be lower for women and non-binary individuals compared to men.

2 In response to comments of the reviewers, we changed the wording, but not the content, of our pre-registered hypotheses in the paper. More specifically, we reformulated pre-registered Hypothesis 1 as current Hypothesis 2, reformulated and integrated pre-registered Hypotheses 3a and 3b into current Hypothesis 1a/b and moved a pre-registered moderation Hypothesis 2 to the supplement (more information about the predicted moderation of social dominance orientation is presented below in section 3).

of stereotypes associated with men and young adults. There is less overlap between stereotypes associated with men and older adults, leading to lower gender prototypicality for older men (Hall et al., 2019).

Compared to young women, the "male as the standard paradigm" and the gender-based social hierarchy (Ridgeway, 2001; Bailey et al., 2019) further suggest that young men are seen as prototypical members of the young age group.

Based on our reasoning regarding the age and gender prototypicality of young men, we expect bias against young male leaders. Both age and gender should contribute to the intersectional bias against young male leaders, but in different ways. While being a man is generally associated with higher status (e.g., Ridgeway, 2001), being young is typically linked to lower status (e.g., Triana et al., 2017). Therefore, only young age should negatively impact the status perception of young male leaders. As such, we hypothesize that "young male leaders" (i.e., being viewed through an intersectional lens) receive more negative evaluations than "male leaders" (i.e., being viewed through a gender lens only), due to lower age-based status ascriptions. Since young male leaders are seen as highly prototypical for the young age group, we do not expect a difference in leader status ascriptions between young male leaders and young leaders in general. We hypothesize:

> *H2: Young male leaders are assigned lower leadership status than male leaders in general.*

3. Overview of the research

To test our hypotheses, we conducted two experimental studies ($N_1 = 918$ and $N_2 = 985$). Both studies adhered to the American Psychological Association (APA) guidelines and obtained approval from the University of Amsterdam's Economics & Business Ethics Committee (protocol numbers: EC 20220209020230 [Study 1], EB-1013 [Study 2]). We determined appropriate sample sizes *a priori* and performed no statistical analyses until all data were collected.

We pre-registered Study 1 using the Psychological Research Preregistration-Quantitative Template (PRP-QUANT; Bosnjak et al., 2022) on the PsychArchives repository.[3] For Study 2, we used the AsPredicted template and pre-registered the study via AsPredicted.[4] We noted the cases where participants were dropped from the sample in line with our pre-registered exclusion criteria.

Additional analyses and results related to a pre-registered hypothesis about the influence of social dominance orientation are provided in the Supplementary material file (sections #2 and #4). The results did not support our hypothesis about the strengthening effect of social dominance orientation in the comparison of young men and men regarding leader status. An interaction effect emerged, however, between social dominance orientation and the comparison of young men and young women's perceived leader status. This finding provides suggestive support for the *subordinate male target hypothesis* (i.e., people with a preference for group-based hierarchy perceive especially male members of non-dominant groups as a threat to their dominant position; e.g., Sidanius and Pratto, 1999). Interestingly, we found suggestive evidence that individuals with a higher social dominance orientation exhibit a stronger bias against young adults. This bias is evident in the lower status ascribed to young leaders compared to male leaders (Study 1, see Supplementary material section #2.2.3), and to young leaders compared to middle-aged leaders (Study 2, see Supplementary material section #4.1.2). The pre-registration documents and Supplementary material can be accessed via the Open Science Framework (OSF) platform using the following link: https://osf.io/gmqt9/?view_only=81b8ac4b5f684d34a311a1c663bfad11.

4. Study 1

In Study 1, we examine our hypotheses regarding the intersection of young age and gender. Specifically, we assess the presence of a gender-specific age bias toward young female leaders (*H1a/b*) and young male leaders (*H2*) by comparing the intersectional lenses to gender and age lenses.

4.1. Methods

4.1.1. Participants

Participants were recruited via the ZPID's PsychLab[5] in collaboration with panel provider Respondi.[6] Data was collected from a heterogeneous sample of U.S. citizens aged 25–69 to ensure generalizability across workplace age groups.[7] For adequate representation of evaluators from various ages and genders within the overall sample, we divided our sample into six evaluator subgroups. Cross-quotas were employed for evaluator age groups and gender across target conditions (i.e., young women and men: 25–39 years; middle-aged women and men: 40–54 years; older women and men: 55–69 years).[8]

An *a priori* power analysis, based on the average effect size from similar previous studies ($f^2 = 0.04$), indicated that 465 participants were needed to achieve 90% power to detect the anticipated small effect at $\alpha = 0.05$ (Faul et al., 2009). In our analyses, we pre-registered comparisons between one target group (e.g., young female targets) and two control groups (e.g., young targets, female targets). We aimed to recruit 180 participants for each target group to ensure sufficient

3 https://doi.org/10.23668/psycharchives.5404

4 https://aspredicted.org/29S_GV2

5 https://leibniz-psychology.org/en/services/data-collection/psychlab-online/

6 https://www.respondi.com/

7 We set the lower age boundary for young adults at 25, as most individuals have entered the workforce by this age. Following the US Discrimination in Employment Act of 1967 (ADEA), we established 39 as the upper boundary for young adults, reflecting those still in the early stages of their careers. Based on the OECD's Directorate for Employment, Labour and Social Affairs, we defined older age in the workplace as beginning at 55. Consequently, we categorized middle-aged adults as those between 40 and 54 years old and older adults as those between 55 and 69, approaching the U.S. retirement age.

8 In the U.S. population, 20.5% are between 25 and 39 years, 18.6% are between 40 and 54 years, and 18.2% are between 55 and 69 years (U.S. Census Bureau, 2021). As young adults (compared to middle-aged and older adults) are only marginally overrepresented in the actual composition of the U.S. population aged 25–69 years, we believe our approach of using similar sample sizes for the three age groups is acceptable.

statistical power. With five target groups, the minimum required number of participants was 900. Deviations from this goal were due to the software employed by the panel provider and outside of our control.

We collected data from 982 participants. Those with incomplete data (i.e., participants who dropped out) were excluded. To ensure high data quality, we excluded 64 participants who incorrectly answered at least one of the two pre-registered understanding and diligence checks (e.g., Gloor et al., 2020; Arthur et al., 2021). Specifically, we excluded 15 participants with insufficient English language proficiency (i.e., those who indicated only basic communication skills/working knowledge [A1 to A2] on an English proficiency item with six response options) and 49 participants who self-reported careless responses ("*should we use your data for our scientific analyses?*," e.g., Aust et al., 2013).

Our analyses were conducted using a final sample size of 918 participants. All participants received the same predetermined payment based on the expected average completion time. The sample was balanced according to our quotas for gender (455 women, 463 men) and age groups (296 young, 311 middle-aged, 311 older). Participants had an average age of 48.20 years ($SD = 12.70$) and were predominantly White (725 White, 59 Asian, 52 Black, 50 Latin, 9 Native American, and 23 unspecified). Most participants were employed (627 participants) in various occupations such as education, manufacturing, and retail, working an average of 37.5 h per week ($SD = 10.8$). Three hundred and four participants had supervisory responsibilities currently (256 participants) or in former positions (48 participants). Participants reported their political orientation using the proxy of right-wing ideology (six-item right-wing authoritarianism scale; Aichholzer and Zeglovits, 2015). In our sample, 30.2% of participants favored right-wing ideology (23.0% slightly, 7.2% somewhat/strongly agree), 50.2% were neutral, and 19.6% opposed right-wing ideologies (14.3% slightly, 5.3% somewhat or strongly disagreed). This distribution corresponds with the political makeup of the general U.S. population (Hawkins et al., 2019).

4.1.2. Design and procedure

We conducted an experimental study using a between-subjects design to evaluate ratings through different lenses: gender (women, men), age (young adults), and intersectionality (young women, young men). The inclusion of gender and age lenses (women, men, young adults) was crucial to determine whether there is an interactive bias resulting from a combination of age and gender biases in the intersectional categories of young women and young men. Participants were randomly assigned to one of the five target groups: women, men, young individuals, young women, and young men.

First, participants read a brief scenario description before rating their assigned target: "On the following pages, you will find a series of attributes commonly used to characterize people in general. We would like you to use this list to tell us how DESIRABLE it is in the workplace for [condition-dependent target group member] to possess the following characteristics. That is, regardless of how [target group] actually is, we want to know how people in the workplace think [target group] SHOULD be. In making your judgments, it may be helpful to imagine that you are about to meet a person in the workplace for the first time, and the only thing you know in advance is that the person is a [target group]." The scenario description was adapted from Schein (1973, 1975) and has been successfully employed in previous research targeting various groups (e.g., Ryan et al., 2011; Morgenroth et al., 2021). For young women, young men, and young adults, the displayed age range was set between 25 and 39 years, following our definition of young adults in the workplace. After rating the attributes (for which results are reported in section #2.3.4 of the Supplementary material as they were not core to our research question), participants were instructed to imagine that the [target group] was their current leader. They rated their target group on our pre-registered dependent variable, perceived leader status. Additionally, we measured other variables not central to our pre-registered hypotheses, such as perceived leader effectiveness and leader liking (see section #2.3.2 in the Supplementary material). The study concluded with a demographic questionnaire.

4.1.3. Measures

4.1.3.1. Perceived leader status

We measured perceived leader status using four items from a scale by Djurdjevic et al. (2017). Participants responded to statements such as, "*This leader possesses high status in my organization*," "*This leader occupies a respected position in my organization*," "*This leader has a position of prestige in my organization*," and "*This leader possesses a high level of prominence in my organization*." Participants used a 7-point scale to indicate perceived leader status (1 = strongly disagree to 7 = strongly agree). Cronbach's alpha for the four leader status items was 0.93.

4.1.3.2. Control variables

We incorporated the evaluator's age and gender as control variables. Research has demonstrated that older evaluators exhibit stronger prescriptive stereotypes for young and older targets (e.g., De Paula Couto and Rothermund, 2019). As individuals age, they may better understand societal expectations for themselves and others, leading to stronger prescriptive stereotypes toward young individuals due to increased experience with and exposure to social norms (Kornadt et al., 2017). Evaluator age was measured as a continuous variable and mean-centered for our analyses. Regarding gender, research indicated that men tend to hold stronger prescriptive stereotypes than women (Martin et al., 2019). Participants identified their own gender using a single item ("please indicate your gender"; woman, man).

4.1.4. Manipulation checks

We asked participants to indicate the age they were thinking about when evaluating the leader ("*In the previous questions, we asked you to think about a specific person as your leader. What age do you think this person would typically have?*"). The differences between the conditions for which age information was presented (i.e., young) versus for those conditions for which no age information was presented were significant. The indicated gender of the leader did not influence the age ascribed to the leader by the participants (see Table 1).

TABLE 1 Study 1: Means and standard deviations of typical age rating for the specific target groups.

	No age info	Young
No gender info	–	30.43^{b} (3.77)
Women	40.61^{a} (7.40)	30.08^{b} (3.69)
Men	41.73^{a} (7.53)	30.23^{b} (4.14)

$N = 918$. Means that share superscripts did not differ at $p < 0.05$ in independent sample t-tests. Standard deviations are reported in brackets.

4.2. Results

4.2.1. Descriptive statistics

We report correlations among the study variables, including demographics (evaluator age, evaluator gender), independent variables (dummy variables for the target groups), and leader evaluations (perceived leader status) in Table 2. Further, we provide mean ratings of perceived leader status by target condition in Table 3.

4.2.2. Preliminary analyses: gender and perceived leader status

Before testing our hypotheses regarding the intersectional effects of young age and gender, we conducted analyses to identify gender differences in perceived leader status for women and men (i.e., when no age information was presented). We conducted independent samples *t*-test using IBM SPSS 29. There was a difference in perceived leader status between men and women, $t(396) = -2.74$, $p = 0.006$, $d = 0.28$, with women scoring higher than men ($M_{diff} = -0.32$, 95% CI [−0.54, −0.09]). We present perceived leader status ratings for different target groups in Figure 1.

4.2.3. Main analyses

We tested our hypotheses using independent samples *t*-tests.[9] In Hypotheses *H1a/b* and *H2*, perceived leader status was the dependent variable. Young women were perceived as having more leader status than young individuals, $t(349) = 2.92$, $p = 0.004$, $d = 0.31$, $M_{diff} = 0.36$, 95% CI [0.12, 0.60], supporting Hypothesis *H1a*. Further, young women were perceived as having less leader status than women in general, $t(363) = -2.17$, $p = 0.031$, $d = -0.23$, $M_{diff} = -0.26$, 95% CI [−0.50, −0.02], supporting Hypothesis *H1b*.

The perceived leader status did not differ between young men and men, $t(370) = -1.68$, $p = 0.093$, $d = -0.18$, $M_{diff} = -0.19$, 95% CI [−0.43, 0.03], failing to support Hypothesis *H2*. Further, young men and young individuals did not differ in perceived leader status, $t(348) = 0.90$, $p = 0.184$, $d = 0.10$, $M_{diff} = 0.11$, 95% CI [−0.13, 0.35].

In addition to our main analyses, we compared the intersectional categories of young women and young men to discern differences *within* this age group. Young women were perceived as having higher leader status than young men, $t(337) = 2.03$, $p = 0.043$, $d = 0.22$, $M_{diff} = 0.25$, 95% CI [0.01, 0.49].

4.3. Discussion (Study 1)

Study 1 provides valuable insights into how different groups are perceived as leaders. Our results indicate that young female leaders are perceived as having a higher status than young leaders, which supports Hypothesis *H1a*. Further, young female leaders were seen as lower in status than female leaders, supporting Hypothesis *H1b*. However, our Hypothesis 2 was not supported. Young male leaders were not perceived as having lower status than male leaders. Finally, we found no difference between the perceived leader status of young male leaders and young leaders, in line with our expectations. Interestingly, our results also revealed a gender difference in perceived leader status, with (young) female leaders scoring higher than (young) male leaders.

To better understand whether the gender-specific age bias affects only young leaders or also applies to middle-aged and older leaders, it is crucial to compare evaluations across all three age groups. These comparisons also allow ruling out alternative explanations, such as the notion that the presence of age information, regardless of whether the leader is young, middle-aged, or older, leads to more negative leader evaluations. Without these comparisons, the assertion that young leaders are evaluated more negatively lacks an appropriate comparative framework. To determine whether the established bias is about young age or age in general and further corroborate our conclusion, we theorize on and examine the age bias toward young leaders compared to middle-aged and older leaders.

In many societies, age-based social hierarchies result in differential access to rewards, power, and privileges for people of various ages

TABLE 3 Study 1: Means and standard deviations of perceived leader status for the specific target groups.

	No age info	Young
No gender info	–	5.17 (1.16)
Women	5.79 (1.16)	5.53 (1.16)
Men	5.48 (1.15)	5.28 (1.11)

$N = 918$. Standard deviations are reported in brackets.

9 Following a reviewer's recommendation, we conducted and reported independent samples *t*-tests in the main text, while offering the pre-registered regression analyses in the Supplementary material in section #2.2. This approach ensures transparency while easing interpretation. The findings and conclusions are the same.

TABLE 2 Study 1: Correlations between study variables.

	1	2	3	4	5	6	7
1. Evaluator age	–						
2. Evaluator gender[a]	0.01	–					
3. Women[b]	−0.01	0.00	–				
4. Men[b]	−0.02	0.01	−0.28**	–			
5. Young adults[b]	0.06	0.04	−0.26**	−0.26**	–		
6. Young women[b]	0.00	−0.01	−0.25**	−0.25**	−0.24**	–	
7. Young men[b]	−0.03	−0.05	−0.25**	−0.25**	−0.24**	−0.23**	–
8. Perceived leader status	−0.03	0.02	0.15**	0.01	−0.12**	0.03	−0.07*

$N = 918$. [a] Women are coded 0, men are coded 1. [b] Each dummy variable groups one target condition (e.g., young adults coded 1) against the other four target conditions (e.g., women, men, young women, and young men coded 0) and therefore provides only limited information regarding bivariate correlations. *$p < 0.05$; **$p < 0.01$.

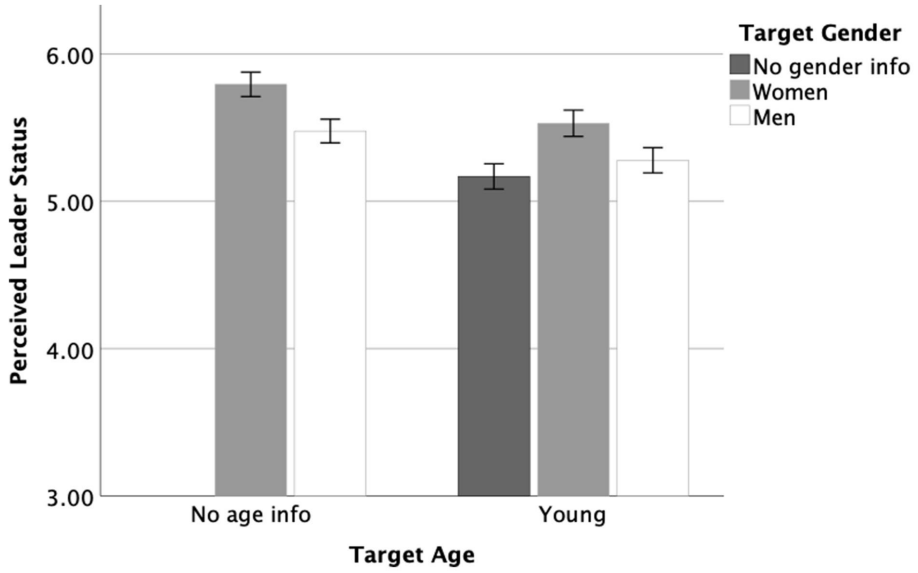

FIGURE 1
Study 1: Results for perceived leader status by target groups. Error bars represent standard errors.

(e.g., Sidanius and Pratto, 1999; Triana et al., 2017). Older adults are often seen as having higher social status than young adults. Older, higher-status individuals are perceived as more competent due to the greater expectations regarding their contributions to a specific group. For instance, leaders' older age can enhance their ability to influence others effectively (e.g., Buengeler et al., 2016), leading to attributions of higher status and competence.

For young leaders, this implies that people may form biased assumptions based on an individual's young age rather than considering young individuals' actual competence, expertise, or other factors relevant to leadership performance (e.g., education, functional background, i.e., specific status characteristics; Lianidou and Zheng, 2022). The lower-status beliefs associated with young age may entail expectations of reduced competence, resulting in limited opportunities and biased evaluations (e.g., Triana et al., 2017). Consequently, these beliefs about young individuals may diminish perceptions of respect and prestige toward young leaders in organizational settings (i.e., ascriptions of leadership status) and negatively affect their perceived competence and expertise (i.e., perceived effectiveness). Therefore, we hypothesize:

> *H3a/b: Young leaders are assigned lower leadership status than (a) middle-aged leaders and (b) older leaders.*

We further investigate how the intersections of age with gender influence perceptions of leader status. While our first study focused on the intersections of young age with gender, as outlined in our Hypotheses *H1a/b* and *H2*, we also consider the alternative explanation that negative perceptions of leader status may be linked to the general presence of age information, regardless of the leader's age. Therefore, we aim to explore the intersectional lens of middle-aged and older age with female (*RQ1a/b*) and male gender (*RQ2a/b*) by proposing the following research questions:

> *RQ1a/b: Do people assign lower leadership status to (a) middle-aged female leaders and (b) older female leaders compared to female leaders in general?*

> *RQ2a/b: Do people assign lower leadership status to (a) middle-aged male leaders and (b) older male leaders compared to male leaders in general?*

5. Study 2

In Study 2, we investigate the potential age bias against young leaders compared to middle-aged and older leaders (*H3a/b*). Second, we test our hypotheses concerning the intersection of young age and gender (*H1a/b*, *H2*) to establish generalizability. Third, we explore the intersection of middle-aged and older age with gender in an exploratory manner (*RQ1a/b* and *RQ2a/b*).

5.1. Methods

5.1.1. Participants

An *a priori* power analysis based on the effect size from Study 1 indicated that 968 participants would be required to achieve 95% power for detecting the anticipated small to medium effect (Cohen's $f = 0.16$) at $\alpha = 0.05$ (Faul et al., 2009). We thus recruited 1000 participants through the panel provider CloudResearch Connect.[10] Participants with incomplete data (i.e., those who dropped out) were excluded from the study.

To maintain high data quality, we excluded 15 participants who failed to correctly answer at least one of the two pre-registered

10 https://connect.cloudresearch.com

TABLE 4 Study 2: Means and standard deviations of typical age rating for the specific target groups.

	No age info	Young	Middle-aged	Older
No gender info	–	27.54[b] (5.47)	45.90[c] (5.61)	56.65[d] (8.43)
Women	40.98[a] (7.40)	27.80[b] (4.33)	45.61[c] (6.06)	54.90[d] (6.65)
Men	41.62[a] (6.97)	28.77[b] (8.84)	45.28[c] (5.67)	56.37[d] (7.54)

$N = 985$. Means that share superscripts did not differ at $p < 0.05$ in independent sample t-tests. Standard deviations are reported in brackets.

understanding and diligence checks (e.g., Gloor et al., 2020; Arthur et al., 2021). This group consisted of five participants with inadequate English language proficiency and 10 participants who self-reported careless responses both determined as in Study 1.

Whereas in Study 1, all age groups were represented equally, in Study 2, we aimed to obtain a representative sample of the U.S. by implementing quotas based on recent U.S. census data, which considered factors such as gender, age, race, and political orientation (U.S. Census Bureau, 2021). Any deviations from the target demographics may have resulted from the panel provider's software limitations and were beyond our control. Our sample included 499 women, 483 men, and three individuals who identified as neither male nor female. The participants' mean age was 42.35 years ($SD = 13.82$), ranging from 18 to 69 years. Regarding racial background, 74.9% identified as White, 11.2% as Black, and 13.1% as Asian, Native American, or another race. Political orientation was distributed as 39.3% conservative, 29.1% moderate, and 31.6% liberal. This methodology ensured generalizable findings that accurately represent the diverse U.S. population.

5.1.2. Design and procedure

We conducted an experimental study with a between-subjects design where participants evaluated a leader belonging to a specific target group. The study is organized into three sub-studies, each focusing on different aspects of the target: (a) gender (two conditions: women, men), (b) age (three conditions: young adult, middle-aged adult, older adult), and (c) intersections of age and gender (six conditions: young women, young men, middle-aged women, middle-aged men, older women, older men).

Participants read the following scenario before rating their target group regarding leader evaluation measures: "On the following pages, you will find a series of statements and questions. When answering these questions, please imagine working in an organization where a [condition-dependent target group member] is your current leader. In making your judgments, it may be helpful to imagine that you are about to meet your leader for the first time, and the only thing you know in advance is that your leader is a [target group]. How do you feel about a [target group] as your current leader?"

5.1.3. Measures

We used the same leader evaluation measures as those employed in Study 1. These measures include perceived leader status (Djurdjevic et al., 2017), perceived leader effectiveness (Giessner and van Knippenberg, 2008; Gündemir et al., 2019), and leader liking (Rudman et al., 2012). Cronbach's alpha for perceived leader status was 0.95. In section #3.1 of the Supplementary material, we provide details on perceived leader effectiveness and leader liking.

5.1.4. Manipulation checks

We asked participants to specify the age they had in mind in their leader evaluations (The question was: "*In the previous questions, we asked you to think about a specific person as your leader. What age do you think this person would typically have?*"). Like in Study 1, we only found significant differences in specified age between the different age conditions. There was no difference in age ratings for male and female leaders (see Table 4). Furthermore, age ratings did not vary within the respective age groups (e.g., young, middle-aged, older), independent of whether these target groups were presented with or without gender information.

5.2. Results

5.2.1. Descriptive statistics

We report correlations among the study variables, including demographics (evaluator age, evaluator gender), independent variables (dummy variables for the target groups), and leader evaluations (perceived leader status) in Table 5. We provide mean ratings of the leader evaluations by target condition in Table 6.

5.2.2. Preliminary analyses: gender and perceived leader status

Before testing our hypotheses, we again conducted preliminary analyses to identify gender differences in leader evaluations for women and men (i.e., when no age information was presented). We conducted independent samples t-tests using IBM SPSS 29. The significantly higher leader status of women as compared to men in Study 1 did not replicate, even though the direction of findings was the same, $t(179) = 1.57$, $p = 0.12$, $d = 0.23$, $Md_{iff} = 0.23$, 95% CI [−0.06, 0.52].

5.2.3. Main analyses

5.2.3.1. Age and perceived leader status

In support of *H3a* and *H3b*, perceived leader status differed between young adults and middle-aged adults, $t(179) = -2.79$, $p = 0.003$, $d = 0.42$, $M_{diff} = -0.45$, 95% CI [−0.77, −0.13], and between young adults and older adults, $t(177) = -4.36$, $p < 0.001$, $d = 0.65$, $M_{diff} = -0.45$, 95% CI [−0.99, −0.37]. Middle-aged and older adults did not differ in perceived leader status, $t(176) = -1.64$, $p = 0.103$, $d = -0.25$, $M_{diff} = -0.23$, 95% CI [−0.50, 0.05].

5.2.3.2. Intersections of young age with gender

An independent sample t-test indicated no differences in perceived leader status between young women and young individuals, $t(178) = 0.40$, $p = 0.692$, $d = 0.06$, $M_{diff} = 0.07$, 95% CI [−0.30, 0.44], which does not support Hypothesis *H1a*. Young women were seen as having lower leader status than women in general, $t(179) = -2.98$, $p = 0.003$, $d = -0.44$, $M_{diff} = -0.52$, 95% CI [−0.87, −0.18], supporting Hypothesis *H1b*.

In line with Hypothesis 2, young men were perceived to possess lower leader status than men in general, $t(173) = -3.84$, $p < 0.001$, $d = -0.58$, $M_{diff} = -0.61$, 95% CI [−0.93, −0.30]. Additionally, there was no difference in perceived leader status between young men and young individuals, $t(175) = -1.39$, $p = 0.168$, $d = -0.21$, $M_{diff} = -0.25$, 95% CI [−0.60, 0.10]. Figure 2 displays the ratings of perceived leader status for the different target groups.

10.3389/fpsyg.2023.1204547

TABLE 5 Study 2: Correlations between study variables.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Evaluator age	–												
2. Evaluator gender[a]	−0.12**	–											
3. Women[b]	−0.01	−0.03	–										
4. Men[b]	−0.01	−0.01	−0.10**	–									
5. Young adults[b]	−0.01	0.02	−0.10**	−0.10**	–								
6. Middle-aged adults[b]	0.01	0.02	−0.10**	−0.10**	−0.10**	–							
7. Older adults[b]	−0.04	0.05	−0.10**	−0.10**	−0.10**	−0.10**	–						
8. Young women[b]	0.00	−0.04	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	–					
9. Young men[b]	0.00	−0.01	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	–				
10. Middle-aged women[b]	0.02	−0.03	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	–			
11. Middle-aged men[b]	0.05	−0.04	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	–		
12. Older women[b]	−0.01	0.09**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	–	
13. Older men[b]	−0.01	−0.01	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	−0.10**	–
14. Perceived leader status	−0.05	0.01	0.07*	0.01	−0.10**	0.03	0.09**	−0.08*	−0.17**	−0.01	0.00	0.06	0.09**

$N = 985$. [a] Women are coded 0, men are coded 1. [b] Each dummy variable groups one target condition (e.g., young adults coded 1) against the other ten target conditions (i.e., all coded 0) and therefore provides only limited information regarding bivariate correlations. *$p < 0.05$; **$p < 0.01$.

TABLE 6 Study 2: Means and standard deviations of perceived leader status for the specific target groups.

	No age info	Young	Middle-aged	Older
No gender info	–	5.06 (1.20)	5.51 (0.98)	5.74 (0.85)
Women	5.66 (1.03)	5.13 (1.32)	5.38 (1.23)	5.62 (1.15)
Men	5.43 (0.94)	4.81 (1.17)	5.42 (0.94)	5.70 (0.85)

$N = 985$. Standard deviations are reported in brackets.

Finally, following our approach in Study 1, we also compared the intersectional categories of young women and young men to identify differences *within* the young adult age group. In contrast to Study 1, the difference was not significant, although the direction of the effect showed that young women received slightly higher leader status ratings than young men, $t(173) = 1.70$, $p = 0.09$, $d = 0.26$, $M_{diff} = 0.32$, 95% CI [−0.05, 0.69].

5.2.4. Additional analyses

5.2.4.1. Intersections of middle age and older age with gender

In addition to our hypothesis tests, we examined the intersectional effects of middle age and older age with gender on perceptions of leader status. This allows examining the alternative explanation that biased perceptions of leader status may not be specific to the intersection of young age with gender but instead be linked to the presence of age information more generally. To test this alternative explanation, we compare the perceived leader status of middle-aged and older women to women (*RQ1a/b*) and middle-aged and older men to men (*RQ2a/b*), respectively. To support the alternative explanation, we should find similar biased perceptions for the intersectional categories of middle-aged/older women and middle-aged/older men as we observed for young women or young men.

The results of independent samples *t*-tests showed no difference in perceived leader status for middle-aged women compared to women in general (*RQ1a*), $t(180) = -1.63$, $p = 0.105$, $d = 0.24$, $M_{diff} = -0.27$, 95% CI [−0.61, 0.06]. Similarly, there was no difference in perceived leader status for older women compared to women in general (*RQ1b*), $t(180) = -0.22$, $p = 0.827$, $d = 0.03$, $M_{diff} = -0.04$, 95% CI [−0.35, 0.28].

Comparing middle-aged and older men to men in general, the results showed no difference in perceived leader status between middle-aged men and men in general (*RQ2a*), $t(177) = -0.07$, $p = 0.942$, $d = 0.01$, $M_{diff} = -0.01$, 95% CI [−0.29, 0.27] and a difference in perceived leader status for older men compared to men in general (*RQ2b*), with higher scores for older men, $t(177) = 2.06$, $p = 0.04$, $d = 0.31$, $M_{diff} = 0.28$, 95% CI [0.01, 0.54].

These results do not support the alternative explanation that simply mentioning age information results in more negative perceptions of leaders.

Additionally, we compared the intersectional categories of middle-aged or older women and men within their own age groups. There were no significant differences in leader status ratings between middle-aged women and middle-aged men, $t(178) = -0.20$, $p = 0.838$, $d = -0.03$, $M_{diff} = -0.03$, 95% CI [−0.36, 0.29]. Similarly, there were no significant differences in leader status ratings between older women and older men, $t(178) = -0.53$, $p = 0.594$, $d = -0.08$, $M_{diff} = -0.08$, 95% CI [−0.38, 0.22].

5.3. Discussion (Study 2)

The findings from Study 2 largely replicate those from Study 1, with two exceptions. We did not find support for Hypothesis *H1a*, as there was no significant difference in perceived leader status between young women and young adults. However, young women were perceived to have lower leader status than women, which supports Hypothesis *H1b*. In line with Hypothesis *H2*, young men were seen as having lower leader status than men, a finding not supported in Study 1. No significant difference was observed between young men and young adults in terms of perceived leader status. In sum, young women were perceived as having lower status than women in general, whereas young men were perceived as having lower status than men in general. Both young women and young men did not differ from young adults in terms of perceived leader status.

Extending Study 1, our findings also supported Hypotheses *H3a* and *H3b*, indicating that leader status is perceived to be lower for young adults compared to middle-aged adults (*H3a*) and older adults (*H3b*). There was no difference between middle-aged and older adults. Our findings regarding the intersectional lenses of middle-aged and older age with gender (*RQ1a/b* and *RQ2a/b*) further revealed that the bias in leader perception is specific to the intersectional lens of *young* age and gender (see *H1b* and *H2*) and not broadly linked to the presence of age information. Contrary to Study 1, in which women were assigned higher leader status than men, we found no difference in perceived leader status between men and women when no age information was presented, even though the direction of findings was the same.

6. General discussion

The primary goal of this research was to develop a gender-specific understanding of the age bias toward young leaders. To examine the age bias toward young female and young male leaders, we integrated the lens-based account of intersectional stereotyping (Petsko et al., 2022) with status ascriptions based on age and gender (status characteristics theory; Berger et al., 1977; Ridgeway et al., 1985). Our findings from comparing various age groups reveal a strong explicit age bias against young leaders compared to middle-aged and older leaders.

The age bias against young leaders prevails even when gender information is considered. Our results show a similar pattern of bias affecting both young women and young men regarding perceived leader status. In particular, the intersectional lenses (i.e., young women or young men) lead to a more negative perception of leader status than the gender lenses (i.e., women or men). However, at least in Study 2, no differences were found between the intersectional and age lenses (young adults), suggesting that the intersectional bias is driven by age.

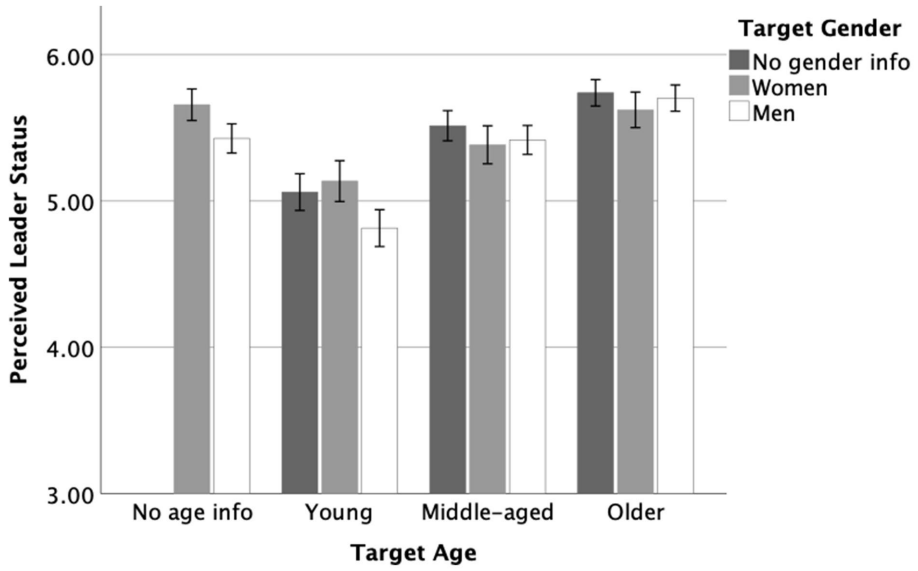

FIGURE 2
Study 2: Results for perceived leader status by target groups. Error bars represent standard errors.

Notably, this bias pattern does not extend to middle-aged or older women and men, bolstering insights into a specific bias against young leaders. Our findings suggest that age plays a major role in leader status perceptions for young women and young men, while it appears to have a minor impact on leader status perceptions of middle-aged and older women or men. These results from Study 2 rule out the alternative explanation that providing age information in general, irrespective of the leader's age, results in more negative evaluations.

6.1. Theoretical implications

Our results have valuable implications. First, there has been a debate about whether bias against members of intersectional group categories is additive or non-additive (e.g., Berdahl and Moore, 2006; Purdie-Vaughns and Eibach, 2008). We hypothesized that the intersectional lens (i.e., young women, young men) elicits status ascriptions that are not simply the average of the singular lenses (young adults, women, or men, respectively). These assumptions were supported for young men. Our findings reveal that the intersectional bias for young men is not simply the algebraic average of biases toward young adults and men since the lowest score is observed for young men (even though previous findings suggest that women should experience more bias than men). This suggests that age bias and gender bias interact in a non-additive manner.

The intersectional bias can be best explained by group prototypicality, as biases become amplified toward a group's most prototypical member (Hall et al., 2019). Stereotypes associated with young adults (e.g., ambitious, self-directed; Francioli and North, 2021) and men (e.g., assertive, agentic; Eagly et al., 2020) may overlap, resulting in a more amplified age bias toward the intersectional category of young men (compared to young women). We found suggestive evidence for the group prototypicality of young men for young adults and young women for women (evident in stereotypical attribute associations such as *dominance*, see section #2.3.4 in the Supplementary material). Contrary to some of our assumptions, it seems that young women face age *and* gender status ascriptions, resulting in an algebraic mean for the intersectional category of young women. However, the differences between young women and young adults (Hypothesis *H1a*) are no longer significant in Study 2, indicating that the results for young women are less clear-cut.

Second, the age bias appears to persist when using an intersectional lens as it shows for both young women and young men. Interestingly, there is a difference in perceived leader status between young women and young men, with young women receiving higher scores in Study 1. However, these differences seem primarily driven by a gender effect, as the patterns in leader perception for women versus men and young women versus young men are quite similar. This suggests that the intersectional bias toward young men and young women is driven by young age. Further, in Study 2, we investigated whether the intersectional effects were specific to young individuals or generalize to middle-aged and older men and women. The findings indicate that biased perceptions of leader status are specific to the intersection of young age and gender, and not broadly associated with the presence of age information. Besides, the effects of gender appear to be more pronounced for young adults than for middle-aged and older adults. As age increases, the leader status perception differences between women and men diminish (i.e., the differences between middle-aged women and middle-aged men or older women and older men are smaller than those between young women and young men).

Third, our results build upon earlier studies showing that young adults in leadership positions are often negatively evaluated (e.g., Buengeler et al., 2016; Kunze and Menges, 2016). In line with our pre-registered hypotheses, we found an age bias specifically targeted at young leaders, as similar biases apparent in lower perceived leader status were not apparent for middle-aged and older leaders. Further, this pattern is consistent across different leadership dimensions, as we observed similar results for perceived leader effectiveness and liking compared to middle-aged leaders (yet not compared to older leaders; see Supplementary material sections #2.3.2 and #4.1.1). Hence, our data also suggest an age bias toward older leaders. Older leaders seemed to be perceived as less effective and likable than middle-aged leaders, although they were not ascribed lower status. These findings tentatively suggest that middle-aged adults may serve as a baseline standard regarding age in the workplace (e.g., Finkelstein et al., 2013), specifically in leadership positions.

Fourth, we did not find support for the expected gender bias against female leaders compared to male leaders. Conversely, compared to male leaders, female leaders were perceived as having more status (Study 1) or equal status (Study 2). One possible explanation is that without a direct threat, such as limited leadership positions, there might be no bias against groups based on static status characteristics such as gender or race (e.g., Kim et al., 2022). Another potential explanation for our findings might stem from participants' awareness of prevalent research and expectations regarding gender stereotypes and bias. This could have led to socially desirable responses in their direct (explicit) leader ratings. We should note that the detection of gender bias can be nuanced, and while we employed direct measures in our studies, such explicit methods might not always fully expose these biases. Therefore, future research could benefit from implementing more indirect (implicit) methodologies akin to those used for uncovering racial bias in leadership studies (e.g., Petsko and Rosette, 2023).

Finally, young age seems to have a stronger impact than gender in leadership roles, at least when bias is assessed directly. This age bias in leadership supports previous research that shows people are likely to endorse age discrimination but not gender discrimination, even if people reject group-based hierarchies (i.e., people with egalitarian views; Martin and North, 2022). The age bias toward young adults also generalizes beyond status ascriptions, as revealed in perceived lower effectiveness and likeability (see Supplementary material sections #2.3.2 and #4.1.1). These encompassing negative evaluations of young leaders are unlikely to be solely due to their (perceived) lack of experience due to their age. While experience is often considered a proxy for competence, it should have less impact on likeability. These additional findings rather suggest an age bias against young leaders based on young age as a diffuse characteristics and therefore independent of an individual's ability and expertise (Lianidou and Zheng, 2022).

6.2. Practical implications

Our results are relevant for optimizing human resource practices in organizations, including recruitment, selection, and performance

evaluation. Whereas some studies found that the impact of age bias and stereotypes on personnel decisions is weak, nonexistent, or inconsistent (Murphy and DeNisi, 2022), other research demonstrates that age stereotypes influence personnel decisions throughout an employee's career (Cadiz et al., 2022). We assume that even small differential treatments resulting from stereotypes can lead to severe consequences in binary decisions (e.g., promotion or dismissal; threshold models of behavior; Hester et al., 2020) or those that generate cumulative (dis) advantages, such as compensation and pay. Rather than focusing on young individuals' actual competencies, expertise, and relevant characteristics for leadership roles (e.g., education, functional background, or specific status characteristics; Lianidou and Zheng, 2022), the lower ascribed status based on the diffuse status characteristic of young age may hinder young individuals from accessing leadership positions, cause biased evaluations, and may lead to a greater chance of dismissal for young leaders. Organizations should account for the age bias in leadership perception by adopting policies and practices that promote age diversity (e.g., Boehm et al., 2014) and incorporate diversity training programs (Homan et al., 2015).

6.3. Limitations and pertinent future research

Our findings stimulate several questions for future research. We focus on age-gender intersectionality while keeping other group categories unspecified (e.g., race). We intentionally used written text for the target group manipulation (e.g., female person, younger female person) rather than images of target group faces (e.g., Spisak et al., 2014), as images could prompt participants to apply a race or intersectional lens containing racial stereotypes, which our research does not address. Considering the importance of race and intersectional categories containing race in leadership perception (e.g., Petsko and Rosette, 2023), future research could address the intersections of young age and race in terms of group prototypicality (Hall et al., 2019) and leadership perception.

In our experimental approach, we asked participants to imagine a young person as their leader. This may add an extra layer of introspection, potentially complicating the evaluation process (i.e., "what it might mean or feel to be managed by a leader younger than oneself"). The impact of additional introspection on evaluations is expected to result in an interaction between evaluator age and leader ratings for young targets, as evaluators' introspective processes, influenced by their own age, may alter their assessments of younger leaders. We tested the interaction of evaluator age on the target group and leader ratings in Study 1 (reported in the Supplementary material, section #2.3.1). However, apart from two exceptions (i.e., leader liking for young women/men compared to women), no interaction effects were identified, indicating limited additional introspection. Future studies could further explore age-inverse leadership relationships, particularly focusing on young leader age in both absolute and relative terms (e.g., Collins et al., 2009; Kunze and Menges, 2016).

7. Conclusion

In this manuscript, we develop a gender-specific understanding of age bias toward young leaders. We uncover an explicit negative age bias toward young leaders when compared to middle-aged and older leaders, a bias which persists across gender (i.e., young female and young male leaders). We examine the intersectional bias toward young female and male leaders by applying the lens-based account of intersectional stereotyping (Petsko et al., 2022). The intersectional lens yields a more negative perception of leader status than the gender lens (i.e., female and male leaders) with no differences between intersectional and age lenses (i.e., young leaders). Moreover, age has more influence, and gender less, for *young* leaders, possibly due to age's less static nature as a status characteristic. Our research emphasizes the importance of considering evaluators' lenses and demonstrates the negative impact of age bias on young leaders.

Data availability statement

The dataset presented in Study 1 can be found at https://doi.org/10.23668/psycharchives.8236. The dataset presented in Study 2 can be found at https://osf.io/gmqt9/?view_only=81b8ac4b5f684d34a311a1c663bfad11.

Ethics statement

Both studies received approval from the University of Amsterdam's Economics & Business Ethics Committee, with protocol numbers EC 20220209020230 for Study 1 and EB-1013 for Study 2. In both studies, participants provided their informed consent to participate.

Author contributions

CD: conceptualization, methodology, data collection, analyses, writing, and editing. CB and AH: conceptualization, methodology, writing, and editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2023.1204547/full#supplementary-material

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Servant versus directive leadership and promotability: does leader gender matter?

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Are leaders more promotable when they show servant or directive leadership – and does this hold for women and men alike? Servant leaders are likely seen as more effective, likable, and thus promotable but less prototypical than directive leaders. We argue that differing degrees of communion (i.e., warmth, morality) and agency (i.e., competence, dominance) underlie the relationship of servant and directive leadership with leaders' promotability. Based on expectancy-violation theory, we assume that men benefit more from servant leadership and women benefit more from directive leadership. Servant leadership aligns more with communion and stereotypes about women. In contrast, directive leadership aligns more with agency and stereotypes about men. These differences may result in gender-biased evaluations threatening fairness in leadership promotions. In a pre-study, servant leadership was more expected of women leaders than of men leaders. However, directive leadership was equally expected of women leaders and men leaders. An experimental vignette study ($N = 454$) revealed that servant leaders were seen as more effective, likable, and promotable than directive leaders, regardless of gender. Perceived leader warmth, morality, and competence were positively, and dominance was negatively, related to leader effectiveness and leader liking, which were positively related to leader promotability. We also investigated whether raters' gender role beliefs influenced the evaluations, which they did not (as reported in the Supplementary material). Concluding, women and men profit equally from exhibiting servant compared to directive leadership.

KEYWORDS

servant leadership, directive leadership, leader promotability, leader effectiveness, leader liking, leader gender, gender stereotypes, expectancy violation theory

Introduction

There is ample evidence on what leadership behaviors benefit organizations and followers (e.g., Judge et al., 2004; Hoch et al., 2018) – but do these behaviors also support a leader's career? Leaders may implement certain leadership behaviors more when these also benefit their promotion. Promotions are often based on evaluating a leader's effectiveness and liking (e.g., Shaughnessy et al., 2011; Hentschel et al., 2018), and leadership behavior is central to this (e.g., Rojahn and Willemsen, 1994; DeRue et al., 2011; Hentschel et al., 2018). Research demonstrates that a follower-oriented leadership behavior, like servant leadership, positively relates to perceived leader effectiveness *and* liking (i.e., high LMX; Hoch et al., 2018; Zhang et al., 2021). *Servant leadership* captures empowering followers and putting their needs first (Eva et al., 2019). In contrast, a more task-oriented behavior like directive leadership primarily focuses on performance-related outcomes by giving orders and monitoring followers (House, 1971; Pearce and Sims, 2002). We argue that servant leaders will be seen as more promotable because they

consider the needs of followers rather than only telling them what to do. Because of these behaviors, they will be seen as more effective in leadership and more likable than directive leaders. However, as directive leaders likely match the typical image of a leader (Northouse, 2016; Offermann and Coats, 2018) more than servant leaders, we expect that they will be seen as more prototypical.

Leader gender might bias the evaluation of servant versus directive leaders' promotability. We expect that both leadership behaviors are contrary in whether they confirm or violate gender stereotypes. Gender stereotypes depict women as more *communal* (e.g., sensitive, nurturing; Eagly et al., 2020). Servant leadership comprises mainly communal, "feminine" behaviors like caring for followers that are more expected of women (Hogue, 2016; Eva et al., 2019). Men are stereotyped as more *agentic* (e.g., assertive, having leadership ability; Prentice and Carranza, 2002; Eagly et al., 2020). Directive leadership captures primarily agentic, "masculine" behaviors like giving orders (Eagly and Johnson, 1990; Pearce and Sims, 2002). Thus, women who show directive leadership and men who show servant leadership are likely perceived to violate gender-role-specific expectations.

Violating expectations either results in an evaluative penalty or a bonus (Jussim et al., 1987). A penalty occurs when an unexpected and negative behavior is shown. When women show agentic behavior that contradicts communion expectations, they are penalized as less likable and promotable than men because such behavior is deemed undesirable for women (*role congruity theory*, Eagly and Karau, 2002; e.g., Rudman et al., 2012; Ma et al., 2022). Similarly, when men show communal behavior that contradicts agency expectations, they are penalized as weak and less likable (Moss-Racusin et al., 2010; Hernandez Bark et al., 2022). A bonus occurs when an unexpected but positive behavior is shown (*expectancy-violation theory*, Jussim et al., 1987; Prentice and Carranza, 2004). Servant and directive leadership are positive behaviors because they benefit followers and organizations (Judge et al., 2004; Hoch et al., 2018). We propose that directive women leaders and servant men leaders exceed typical expectations positively. They are seen as combining communion with agency, or vice versa, resulting in a more favorable evaluation (Prentice and Carranza, 2004). Thus, we expect that directive women leaders receive an *agency bonus* compared to directive men leaders, while servant men leaders receive a *communion bonus* compared to servant women leaders. The bonus should be evident in higher ratings of leader effectiveness, liking, and promotability. Yet, due to the perceived incongruence of their leadership behavior with their gender role, directive women leaders and servant men leaders are likely deemed as less typical leaders. Thus, we expect them to receive lower ratings of leader prototypicality than stereotype-conforming leaders.

In conclusion, our first aim is to examine how servant and directive leadership relate to a leader's promotability due to higher perceived leader effectiveness and liking. Differences in perceived leader communion and agency may drive these relationships. Thus, we examine whether communion and agency are the underlying mechanisms of these evaluations. We follow recent evidence (Hentschel et al., 2019; Ma et al., 2022) as we examine the facets of communion (i.e., warmth and morality) and agency (i.e., competence and dominance; Abele et al., 2016; Rosette et al., 2016) rather than less fine-grained overarching factors. Our second aim is to examine leader gender as a contingency factor, as research suggests that the evaluation of communal and agentic behavior varies according to leader gender (Biernat, 2012; Hentschel et al., 2018). We implement an experimental vignette study in which we manipulate leadership behavior and leader gender using written scenarios. Figure 1 summarizes the hypothesized overall research model.

Our research makes important contributions. First, we add to research on the outcomes of servant as compared to directive leadership by examining their relationships with leader promotability (Judge et al., 2004; Hoch et al., 2018; Eva et al., 2019). There is clear evidence on the benefits of servant leadership for individuals, teams, and organizations. Yet, it remains unclear whether servant leadership helps leaders to advance their careers. We contribute knowledge on how much leaders themselves profit from servant leadership compared to directive leadership, a more typical leadership behavior. In this regard, we shed light on whether servant leadership serves not only organizations and followers but also leaders.

Second, we clarify the mechanisms underlying servant and directive leadership evaluations. We examine whether perceptions of leaders' communion and agency explain the relationship between leadership behavior and perceived leader effectiveness, liking, and promotability. Hereby, we expand knowledge on how leaders can be perceived as effective and likable to receive promotion (Rojahn and Willemsen, 1994; Gartzia and Van Knippenberg, 2016; Hentschel et al., 2018). We add to existing research and evidence on the benefits of examining the facets of communion and agency (Hentschel et al., 2019; Ma et al., 2022).

Third, we contribute to the literature on gender-biased leadership evaluations.[1] We integrate expectancy-violation theory (Jussim et al., 1987; Prentice and Carranza, 2004) with role congruity theory (Eagly and Karau, 2002). Doing so, we theorize and provide evidence on whether and why women and men are rewarded for gender role-incongruent leadership behavior. As we examine evaluative consequences of servant leadership for women versus men, we answer calls for research on gender and servant leadership (Eva et al., 2019) and on male communion bonus in leadership (Hentschel et al., 2018). It is important to investigate whether men receive better evaluations than women for the same leadership behavior or vice versa because such bias threatens gender equity in leadership promotions and positions.

Leadership behavior and leader evaluations

Leadership behaviors are behavioral patterns by which leaders seek to influence their followers (Yukl, 1989). Decades ago, McGregor (1960) proposed that leaders differ in their understanding of followers and how they must be led to produce the best results. Leaders could implement a follower-oriented approach by supporting the needs of followers or a task-oriented approach by directing and monitoring followers. While servant leadership is more follower-oriented and thus a communal leadership behavior (Hogue, 2016), directive leadership is more task-oriented and thus an agentic leadership behavior (Eagly and Johnson, 1990; Pearce and Sims, 2002).

1 We use the term "gender-biased" in combination with evaluation when referring to different evaluations of women and men as leaders. We do not refer to differences in the evaluation behavior of women or men who rate these leaders.

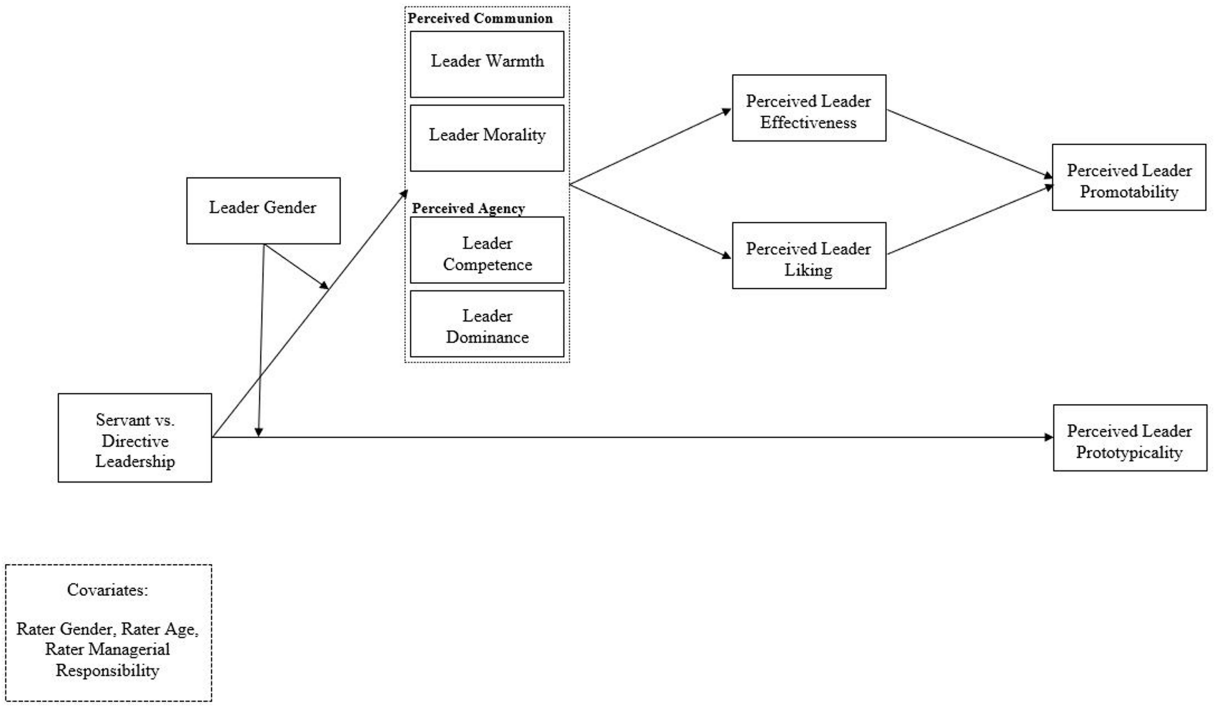

FIGURE 1
Hypothesized overall research model.

Servant leadership

By putting followers first and focusing on their growth, servant leaders empower them to develop their best potential (Eva et al., 2019). In addition, servant leaders encourage followers to dedicate themselves beyond their self-interest to the wider community and organization (Eva et al., 2019). Servant leadership positively relates to follower's job satisfaction, leader effectiveness, and leader liking (i.e., high LMX; Hoch et al., 2018; Zhang et al., 2021).

Directive leadership

Directive leadership involves setting goals, directing, and monitoring followers (House, 1996; Pearce and Sims, 2002). Directive forms of leading are positively related to follower job satisfaction, satisfaction with the leader, motivation, and leader effectiveness (House, 1971; Judge et al., 2004). However, directive leadership does not promote followers' liking of their leader (Peterson, 1997).

Leadership behavior and promotability

Leader promotability is an important parameter for evaluating how much leaders themselves benefit from showing certain leadership behaviors. Leader promotability captures perceptions of a leader's capability to ascend the organizational ladder (Ma et al., 2022). Communal behaviors more positively predict leader effectiveness than agentic behaviors (Judge et al., 2004). Because servant leaders support followers' needs, they are likely seen as more effective and as more likable than directive leaders. Being seen as effective and likable positively relates to promotability (e.g., Shaughnessy et al., 2011; Hentschel et al., 2018). Thus, we argue that servant leadership is related to higher perceptions of leader effectiveness, liking, and promotability than directive leadership.

Leadership behavior and leader prototypicality

Leader prototypicality reflects how much a certain leadership behavior aligns with the typical image of a leader.[2] Stereotypes toward leaders, so-called *leader prototypes* (implicit leadership theories; Lord et al., 1984; Offermann and Coats, 2018), reflect people's shared beliefs about the characteristics of leaders and leadership behavior. Raters assess leaders' prototypicality by comparing them with these leader prototypes (*leadership categorization theory*, Lord et al., 1984; Lord and Maher, 1991). Apart from communal characteristics like sensitivity or dedication, agentic characteristics like strength or tyranny are overrepresented in leader prototypes and still deemed

2 In line with Van Knippenberg and Van Knippenberg (2005), we use the term leader prototypicality referring to "the leader's representativeness of a leader category (i.e., matching the stereotype of a leader)" (p. 27) as described in leadership-categorization theory. To avoid confusion, we distinguish this conceptualization of leader prototypicality from the concept of group prototypicality that is used in social-identity analysis and refers to a leader's "representativeness of the work group, team, or organization that the leader is leading" (Van Knippenberg and Van Knippenberg, 2005, p. 27). We concentrate on prototypicality concerning typical leaders (Lord et al., 1984; Barsalou, 1985; Junker and Van Dick, 2014; Van Quaquebeke et al., 2014) because compared to the ideal leader prototype, the typical leader prototype includes more ineffective characteristics and thus reflects the general image of a leader (Schyns and Schilling, 2011). In addition, the typical leader prototype comprises more agentic characteristics (Epitropaki and Martin, 2004; Offermann and Coats, 2018) and raters believe that, first and foremost, agency is related to the leader role (Eagly and Karau, 2002).

more typical of a leader (Koenig et al., 2011; Offermann and Coats, 2018). Thus, we argue that servant leadership is perceived as less prototypical than directive leadership.

> *Hypothesis* 1: Servant leadership compared to directive leadership relates more positively to perceived leader effectiveness (H1a), liking (H1b), and promotability (H1c) but less positively to perceived leader prototypicality (H1d).

Leadership behavior, leader evaluations, and leader gender

Leadership behavior and leader gender

Leadership behaviors are perceived as more or less stereotypically "feminine" or "masculine" (see Kark et al., 2023) and thus as rather congruent or incongruent with gender stereotypes (Eagly and Karau, 2002). Servant leadership is congruent with the "feminine" gender role (Hogue, 2016; Lemoine and Blum, 2021), whereas directive leadership is congruent with the "masculine" gender role and the leader role (Eagly and Johnson, 1990; Eagly and Karau, 2002). Research suggests that women leaders are expected to enact more servant leadership, while men leaders are expected to show more agentic leadership behavior (Hogue, 2016), such as directive leadership. But how are women and men leaders evaluated when showing gender role (in)congruent leadership behavior?

Results on the evaluation of gender role (in)congruent behavior so far were inconsistent. Some research hints at a penalty evident in lower perceived liking and hireability ratings for agentic women than agentic men (e.g., Rudman, 1998; Rudman et al., 2012). Yet, recent research suggests a promotability bonus for agentic women (Ma et al., 2022). For communal men, some research suggests that these men were seen as less likable but not as less competent or hirable than communal women (Moss-Racusin et al., 2010; Hernandez Bark et al., 2022). Other research suggests a bonus for communal men leaders compared to communal women leaders in the form of higher perceived leader effectiveness and promotability (Hentschel et al., 2018).

Leadership behavior, leader gender, and expectancy-violation theory

We argue that servant men leaders and directive women leaders receive an evaluative bonus compared to stereotype-conforming leaders (servant women leaders and directive men leaders). To explain whether a bonus or penalty occurs, expectancy-violation theory (Jussim et al., 1987; Prentice and Carranza, 2004) distinguishes whether a *descriptive*, *prescriptive*, or *proscriptive* gender stereotype is violated (Prentice and Carranza, 2004). *Descriptive* gender stereotypes reflect how women/men typically are. *Prescriptive* gender stereotypes capture how women/men ideally should be. Finally, *proscriptive* gender stereotypes reflect how women/men ought not to be (Burgess and Borgida, 1999; Heilman, 2012; Rudman et al., 2012). A penalty occurs for violating prescriptive or proscriptive gender stereotypes, evident in lower social attractiveness and popularity (Eagly and Karau, 2002; Prentice and Carranza, 2004; see Rudman and Glick, 2001). A penalty also occurs for violating a descriptive gender stereotype by exhibiting a *negative* attribute deemed undesirable in society (Jussim et al., 1987; Prentice and Carranza, 2004). Yet, a bonus occurs when one violates descriptive gender stereotypes and thus raters' expectations by exhibiting a *positive* attribute that is generally seen as desirable (Jussim et al., 1987; Bettencourt et al., 1997). Servant men leaders and directive women leaders violate the expectation that women are typically not agentic and that men are typically not communal. These violations likely result in a bonus, as servant and directive leadership are positive behaviors. Servant men leaders might be perceived as agentic (because of gender stereotypes) but also as communal (due to their leadership behavior). Directive women leaders might be seen as agentic (due to their leadership behavior) and as communal (because of gender stereotypes).

Leadership behavior, leader gender, leader evaluations, leader promotability, and prototypicality

We propose that servant men leaders and directive women leaders score higher on perceived leader effectiveness, liking, and promotability but lower on leader prototypicality than servant women leaders and directive men leaders. Violating descriptive stereotypes has a more extreme impact on evaluations than confirming stereotypes (Jussim et al., 1987). Thus, servant men leaders and directive women leaders are likely seen as more effective and likable than their stereotype-conforming counterparts. Since leader effectiveness and liking are related to promotability (Shaughnessy et al., 2011; Hentschel et al., 2018), we expect that this evaluative bonus is also evident in leaders' promotability. Yet, due to the perceived incongruence between servant leadership behavior and men's agentic gender roles, we expect servant men leaders to score lower on perceived leader prototypicality than servant women leaders. Due to the perceived incongruence between directive leadership behavior and women's communal gender roles, we expect directive women leaders to score lower on perceived leader prototypicality than directive men leaders.

> *Hypothesis* 2: For men (women) leaders as compared to women (men) leaders, servant (directive) leadership relates more positively to perceived leader effectiveness (H2a), liking (H2b), and promotability (H2c) but less positively to perceived leader prototypicality (H2d).

The mediating role of perceived communion and agency

Servant and directive leadership, communion, agency, and leader promotability

We propose that communion and agency underlie the relationship of servant and directive leadership behavior with perceived leader effectiveness and liking, which, in turn, predict leader promotability. Communion and agency are composed of facets. Distinguishing these facets offers a more differentiated view because the facets differ in their social desirability and whether they are prescribed or proscribed for women and men (Rudman et al., 2012; Hentschel et al., 2019; Ma et al., 2022). As a result, the facets differ according to whether a positive or negative violation occurs.

Communion and agency

Communion contains warmth and morality (Abele et al., 2008, 2016). *Warmth* is the ability to connect and cooperate with other

people, while *morality* captures a person's perceived trustworthiness and correctness (Brambilla et al., 2011). Communion is linked to be seen as effective, and likable, and to leader promotability (Wojciszke et al., 2009; Hentschel et al., 2018). Agency generally comprises competence (Abele et al., 2016, 2021) and dominance (Rudman and Glick, 2001; Rosette et al., 2016). *Competence* refers to a person's task-based talents and skills (Abele et al., 2016) and relates to a person's perceived leader effectiveness, liking, and promotability (Singh and Tor, 2008; Dulebohn et al., 2017; Hu et al., 2022; Ma et al., 2022). *Dominance* is a person's tendency to control and exercise influence and authority over others (Rosette et al., 2016). Dominance is part of destructive leadership (Padilla et al., 2007) and, unsurprisingly, holds a null or negative relationship with perceived leader liking (Cheng et al., 2013), and a negative relationship with leader promotability (Ma et al., 2022).

Leadership behavior, communion, and gender-biased leadership evaluations

We argue that leader gender influences the relationship of servant and directive leadership with communion in terms of perceived warmth and morality. We expect that servant leadership positively predicts perceptions of leader warmth and morality as servant leadership is a communal leadership behavior. Warmth and morality include behaviors prescribed for women but not proscribed for men (Prentice and Carranza, 2002; Abele et al., 2008, 2021). Thus, following the assumptions of expectancy-violation theory (Prentice and Carranza, 2004) and role congruity theory (Eagly and Karau, 2002), we argue that women displaying servant leadership evade a penalty as servant leadership aligns with communion. We expect that servant men leaders receive a bonus as they positively violate expectations that they are low on communion. Interestingly, women and men are evaluated according to stereotypes for their gender group (*shifting standards theory*; Biernat, 2012). Men showing warmth and morality are likely perceived as especially warm and moral for men, while women doing the same are perceived as averagely warm and moral for women. Thus, we expect that the positive relationship of servant vs. directive leadership with warmth and morality is stronger for men leaders compared to women leaders. Being seen as warm and moral positively relates to leader effectiveness, liking, and, consequently, promotability (Wojciszke et al., 2009; Shaughnessy et al., 2011; Hentschel et al., 2018). Thus, we propose:

> *Hypothesis* 3: Servant (compared to directive) leadership positively relates to perceptions of leader warmth (H3a) and morality (H3b), which, in turn, positively relate to perceived leader effectiveness and liking, and, ultimately, to promotability. These mediation effects are stronger for men leaders compared to women leaders.

Leadership behavior, agency, and gender-biased leadership evaluations

We argue that leader gender influences the relationship of servant and directive leadership with perceived competence and dominance. We expect that servant leadership positively relates to perceived leader competence and negatively to dominance. Competence and dominance differ in their gendered prescription and proscription. Omitting these differences in previous research and that competence is socially desirable while dominance is undesirable might be one reason for inconclusive findings regarding women's agency bonus and penalty (Ma et al., 2022). Competence is prescribed for men but neither prescribed nor proscribed for women (Rudman et al., 2012). Thus, women leaders receive a bonus for displaying competence (Prentice and Carranza, 2004; e.g., Ma et al., 2022). Dominance is prescribed for men given their higher status in society but proscribed for women given their lower status in society (*status incongruity hypothesis*, Rudman et al., 2012). Thus, dominance is even more negatively linked to perceived promotability for women leaders than for men leaders (Ma et al., 2022). Due to shifting gender standards for competence (Biernat, 2012), women displaying competence are likely perceived as especially competent for women, while men doing the same are perceived as averagely competent for men. Thus, we propose that the positive relationship between servant vs. directive leadership behavior and competence is stronger for women leaders than for men leaders. As men in general are seen as more dominant than women due to gender stereotypes (i.e., agentic; Eagly et al., 2020), servant men leaders are likely perceived as more dominant than servant women leaders. Thus, we expect that the negative relationship between servant vs. directive leadership behavior and dominance is stronger for women leaders than for men leaders. Being seen as competent positively, and as dominant negatively, relates to leader effectiveness, liking, and, consequently, promotability (Singh and Tor, 2008; Shaughnessy et al., 2011; Cheng et al., 2013; Dulebohn et al., 2017; Hentschel et al., 2018; Hu et al., 2022; Ma et al., 2022). Thus, we propose:

> *Hypothesis* 4: Servant (compared to directive) leadership positively relates to perceptions of leader competence (H4a) and negatively relates to perceptions of leader dominance (H4b). In turn, competence positively and dominance negatively relate to perceived leader effectiveness and liking, and, ultimately, to promotability. These mediation effects are stronger for women leaders compared to men leaders.

Overview of studies

Before testing our hypotheses, we conducted two pre-studies. Pre-study 1 concerns gender-biased leadership expectations. Pre-study 2 validates the visual stimulus material of two silhouettes used in the main study.

Additional analyses and results regarding our hypothesis about the moderating role of raters' gender role beliefs can be found in the Supplementary material (section #3.2.2). Raters may differ whether they evaluate a gender stereotype violation as positive or negative depending on their gender role beliefs (role congruity theory, Eagly and Karau, 2002). We assessed raters' egalitarian gender role beliefs via Larsen and Long's (1988) 20-item comprising *Attitudes toward Sex Roles Scale*. The results did not support our hypothesis about raters with traditional beliefs giving more unfavorable and with egalitarian beliefs giving more favorable evaluations for stereotype-violating leaders compared to stereotype-conforming leaders. Due to the high skewness of our data toward egalitarian gender role beliefs, the analyses and results must be interpreted with caution and were moved to the Supplementary material during the revision process. Thus, we can neither support nor reject the suggestion that raters' gender role beliefs may evoke gender bias in the evaluation of servant or directive leaders. In the Supplementary material (section #3.2.2),

we further elaborate on the potential demand effects that might have occurred for the scale of gender role beliefs.

Pre-study 1

Expectations of leader gender and leadership behaviors

We investigated whether women are expected to exhibit more servant leadership than men and whether men are expected to show more directive leadership than women. Specifically, we investigated descriptive, *typical* leadership expectations representing leadership behaviors that women and men are expected to show typically. We also investigated prescriptive, *ideal* leadership expectations representing leadership behaviors women and men should ideally show.

Method

We conducted a 2 (leader gender: woman, man) × 2 (expectation: typical, ideal) experiment with leader gender varying within-subject and expectations varying between-subject. We recruited an online sample in Germany and randomly assigned participants to one of two conditions, *typical* ($N = 44$, 70.5% female, 2 participants did not indicate their gender, $M_{age} = 28.95$ years, $SD_{age} = 8.97$) or *ideal* ($N = 48$, 77.1% female, $M_{age} = 28.65$ years, $SD_{age} = 9.82$) leadership expectations. In each condition, we randomized whether participants had to first answer for women leaders or men leaders, with a distractor task in-between (see Supplementary material, section #1.2). The instruction for the typical/ideal condition was: "The following refers to your expectations regarding typical/ideal behavior. Please imagine having a woman/man as your formal supervisor." We chose this instruction as imagining a woman/man as formal supervisor corresponds to the scenario manipulation we used in the main study. The typical condition represented descriptive leadership stereotypes ("What kind of leadership behavior does a woman/man typically exhibit?"), while the ideal condition represented prescriptive leadership stereotypes ("What kind of leadership behavior does a woman/man ideally exhibit?"). *Servant leadership* was operationalized by the seven items of the SL-7 (Liden et al., 2015; Ruthus, 2019), with one item being adapted to "I can seek help from her/him if I have a personal problem." *Directive leadership* was measured by five items taken and adapted from Northouse (2016; e.g., "She/He lets me know what is expected of me").[3] Participants indicated on a 7-point Likert scale from (1) *do not agree at all* to (7) *totally agree* on how much they agreed with the presented leadership items.

Do people believe women to (typically and ideally) show more servant leadership? Results

Concerning *typical* leadership expectations, the paired *t*-test indicated that women were expected to typically show more servant leadership ($M = 4.93$, $SD = 0.74$) than men ($M = 3.98$, $SD = 0.82$, $t(43) = 8.12$, $p < 0.001$). Concerning *ideal* leadership expectations,[4] women should ideally show more servant leadership ($M = 5.26$, $SD = 0.72$) than men ($M = 4.89$, $SD = 1.01$, $t(47) = 3.53$, $p < 0.01$; see Figure 2).

Do people believe men to (typically and ideally) show more directive leadership? Results

Concerning *typical* leadership expectations, women ($M = 5.41$, $SD = 0.66$) and men ($M = 5.28$, $SD = 0.86$, $t(43) = 1.29$, $p = 0.20$) were equally expected to typically show directive leadership. We also found no differences in *ideal* leadership expectations as men ($M = 5.65$, $SD = 0.81$) and women ($M = 5.64$, $SD = 0.78$, $t(47) = 0.09$, $p = 0.93$; see Figure 3) were equally expected to ideally show directive leadership.

Pre-study 2

Validation of silhouettes

To increase gender salience regarding our leadership scenario in the main study, we validated female and male visual stimuli for leader gender. One more realistic option was a female and a male face (following Buengeler et al., 2016; generated from several pictures taken from DeBruine and Jones (2017) using the tool *WebMorph* (DeBruine, 2018), see Supplementary material, section #2.2). The other more abstract option was a female and a male silhouette (adapted from Hernandez Bark et al., 2022). We adapted the female silhouette by inserting it in a blank background so that it was presented on a blank background like the male silhouette.

Method

We recruited an online sample in Germany ($N = 42$, 52.4% female, 38.1% male, 4.8% diverse, 4.8% did not specify their gender; $M_{age} = 38.27$ years ($SD = 14.62$), 1 participant did not indicate the own age). We presented participants with a female and a male person via a face and a silhouette. Participants saw the female and male face as well as the female and male silhouette. We randomly assigned whether the faces or silhouettes were presented first. Within the faces and silhouettes condition we randomized which gender was displayed first. A distractor task was inserted between the faces and silhouettes (see Supplementary material, section #2.2). Regarding the presented stimuli, participants indicated the person's perceived attractiveness, intelligence, liking, dominance, competence, warmth, and morality, as well as how friendly they would treat the person and how much they would be interested in getting to know the person on a 5-point Likert scale. Additionally, they indicated the perceived age and perceived gender of the presented stimuli. The questions were created by the authors, were presented in a randomized order, and are listed in the Supplementary material (section #2.2).

Results

The female and the male face differed substantially (see results in the Supplementary material, section #2.3), so we focused

3 The reversed item was excluded because the corrected item-total correlation was below 0.30 and Cronbach's alpha was better when the item was deleted (Field, 2018; see Supplementary material, section #1.2).

4 For the prescriptive servant and directive leadership condition, the Shapiro–Wilk test indicated that the differences between the scores for women and men were non-normally distributed ($p < 0.001$) which is negligible as our sample size exceeded $n = 30$ (Stone, 2010). Outliers remained in the analyses as results did not differ when they were excluded.

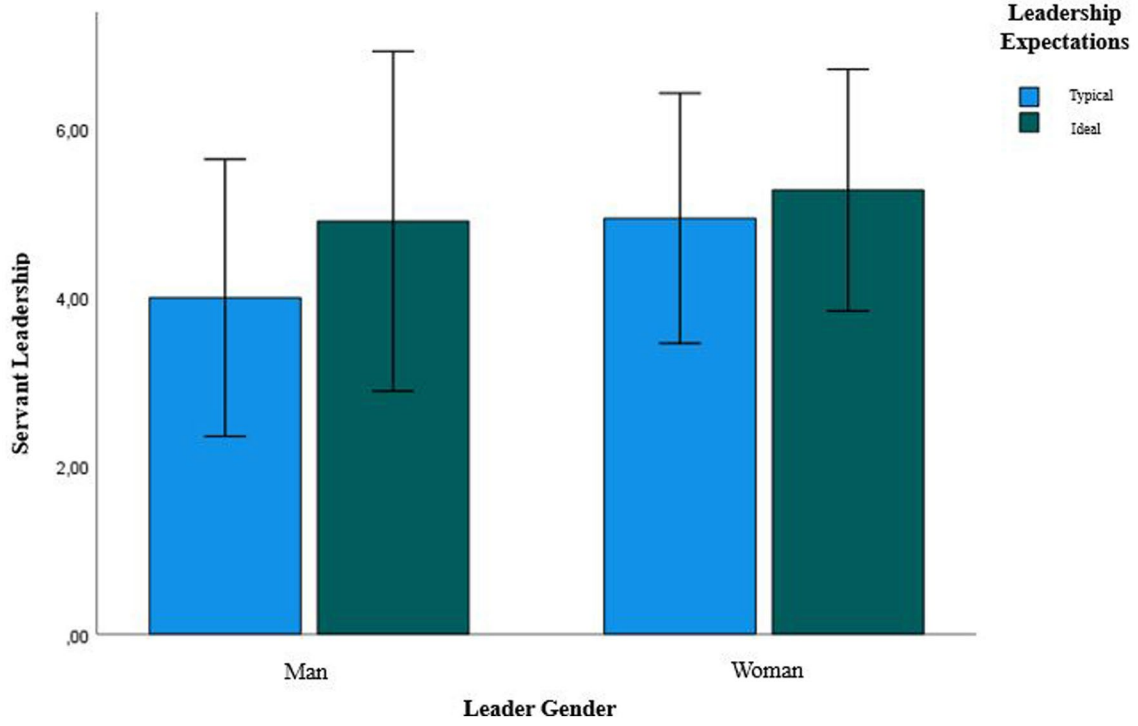

FIGURE 2
Bar plot showing how much servant leadership is typically and ideally expected of women leaders and men leaders.

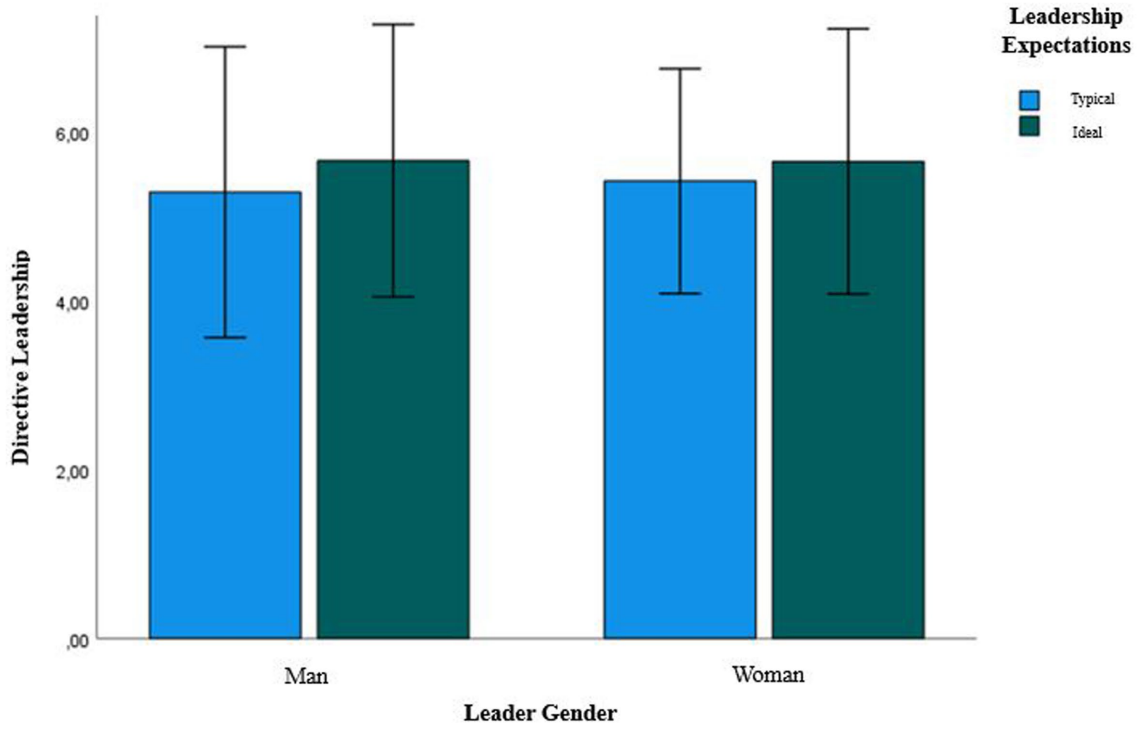

FIGURE 3
Bar plot showing how much directive leadership is typically and ideally expected of women leaders and men leaders.

on silhouettes for the stimulus material. The paired *t*-tests indicated no differences between the silhouettes except regarding their perceived gender and gender stereotypes (see Table 1). The female silhouette was perceived to be warmer and more moral than the male. The male silhouette was perceived to be more dominant.

Method and materials

Sample and design

To test our hypotheses, we conducted an experimental online study. The 2 × 2 design is based on two independent variables: leader's leadership behavior (servant vs. directive leadership) and leader gender (woman vs. man). The total sample consisted of $N = 454$ full-time working employees (>29 h/week) after excluding participants who failed manipulation and quality checks during the survey (see procedure and manipulation, see manipulation checks).[5] Participants needed to be German native speakers to ensure their susceptibility to the gendered language used in the study's manipulation and questionnaires.[6] Two hundred twenty seven participants were women (50.00%), and the mean age was 45.92 years ($SD = 11.66$). On average, participants worked 39.68 h per week ($SD = 4.71$). Participants' highest education was vocational training (27.1%), intermediate school leaving certificate (19.4%), university of applied sciences degree (18.7%), advanced school leaving certificate (14.1%), university degree (14.1%), lower secondary education (5.1%), and a Ph.D. degree (1.5%). One hundred twenty one participants held a supervisory position themselves (26.7%). Most participants indicated that they have or had a formal supervisor at work (96.5%). Two hundred fifty five of the participants indicated that they thought about their (former) supervisor during the survey (56.2%), while 199 participants indicated that they did not think about any (former) supervisor (43.8%, 1 of these never had any supervisor). Most participants indicated that they could imagine the presented scenario very well, well, or moderately well (93.1%); only 31 participants found it difficult or very difficult (6.9%).[7]

Procedure and manipulation

In the online survey, we informed participants that we were interested in their evaluation of a leadership scenario. Then, they were divided according to their gender and randomly assigned to one of four manipulation conditions, to ensure a nearly equal number of women and men across conditions. We took this measure to counterbalance participant gender. All participants then read the instruction: "The following text describes a situation in the workplace. Please read the text on the next page carefully. It is important that you put yourself in the scenario described. Please imagine that the person described is your formal supervisor in real life."

Each condition included a written scenario in which the respective supervisor was either a woman or a man. The female or male silhouette accompanied scenarios to increase gender salience (see Pre-Study 2). In addition, we used the gendered nature of the German language. The female or male version of "supervisor" highlighted the respective gender and was accompanied by the gendered possessive pronoun "your" (*Ihre Vorgesetzte* or *Ihr Vorgesetzter)*. The translated version of the scenarios is depicted in Table 2. Each scenario started with "You work full time in an organization. In the picture, you see your formal supervisor." The female or male silhouette was presented below, followed by the manipulation of the leadership behavior and leader gender.

Manipulation checks

We employed instructional manipulation checks regarding the characteristics of the person described in the scenario to ensure that participants understood the manipulation correctly (Oppenheimer et al., 2009). We asked for the gender (woman, man, no gender mentioned, I do not know), the organizational position (own supervisor, colleague, CEO of company), and the general leadership behavior (follower-focused, task-focused, I do not know) of the person depicted in the scenario (see Supplementary material, section #3.1). Participants who failed to respond correctly could not continue with the survey.[8] In addition, we were interested in how much participants perceived the described supervisor to exhibit servant and/or directive leadership. Participants assessed the perceived leadership behavior by replying to four items for each behavior on a 7-point Likert scale (1 = *do not agree at all* to 7 = *totally agree*). From the SL-7 we selected four items with the highest factor loadings (Liden et al., 2015; items 2, 3, 5, 6). From the directive leadership items (Northouse, 2016), we took all but the reversed item because of its' low item-total correlation in Pre-Study 1. A Welch-test showed differing servant leadership perceptions between the servant and directive leadership condition (95% CI [−3.44, −3.04], $t(439.05) = -32.23$, $p < 0.001$). We also found differing directive leadership perceptions between the servant and directive leadership condition (95% CI [1.27, 1.66], $t(451.38) = 14.94$, $p < 0.001$; for means per condition, see Table 3).[9]

5 We recruited participants via the acquisition platform *Respondi* in exchange for a participation fee. Pre-selection criteria for our online survey included age and working hours per week to ensure that participants are aged 18 to 67 years and are full-time employed at an organization or public service and thus are used to organizational hierarchies.

6 To prevent careless responding, we applied recommendations for prevention and precaution of Goldammer et al. (2020); e.g., payment for participation, providing personal instructions. Initially, we collected data from 460 persons who completed the full questionnaire. At the end of the survey, we asked participants to indicate whether they filled out the questionnaire sincerely so that their data can be used for statistical analyses, with no consequences for their reward. Six participants indicated that they were just clicking through and were excluded from the analyses (Aust et al., 2013).

7 The results of the hypotheses did not differ when the 31 participants were excluded that indicated a difficult or very difficult imagination of the scenario.

8 We discuss the potential of demand effects for our measurement of gender role beliefs in the Supplementary material (section #3.2.2) because these manipulation checks took place before participants had to answer the scale about gender role beliefs. We also computed the analyses of H1 to H4 for the sample that included participants who failed the manipulation checks ($N = 740$). The results for the hypotheses tests did not differ.

9 Hentschel et al. (2018) excluded participants who failed to have a mean difference of one scale point in the direction of the intended leadership behavior. If we had followed their procedure, our sample would have been reduced to $N = 337$. To secure the power of our analyses, we calculated the results with the larger sample. A servant leader may be perceived as giving task-directed orders and clearly formulating expectations, despite these behaviors not being mentioned in the scenario. As all participants had correctly answered the general manipulation check regarding the described leadership behavior, they should have understood the manipulation as intended. However,

TABLE 1 Means and standard deviations for the female silhouette and the male silhouette.

Measures	Condition				
	Female		Male		
	M	*SD*	*M*	*SD*	Paired *t*-test
Perceived attractiveness	3.45	0.63	3.40	0.73	$t(41) = 0.42$, $p = 0.68$
Perceived intelligence	3.62	0.54	3.67	0.65	$t(41) = 0.63$, $p = 0.53$
Perceived liking	3.17	0.49	3.00	0.63	$t(41) = 1.64$, $p = 0.11$
Interest in getting to know the person	3.12	0.74	2.81	0.92	$t(41) = 1.87$, $p = 0.07$
Treating the person in a friendly manner	3.69	0.47	3.64	0.49	$t(41) = 0.81$, $p = 0.42$
Perceived dominance	3.26	0.63	3.62	0.62	$t(41) = 2.64$*, $p = 0.01$
Perceived competence	3.69	0.64	3.60	0.73	$t(41) = 0.94$, $p = 0.35$
Perceived warmth	3.02	0.52	2.69	0.64	$t(41) = 2.65$*, $p = 0.01$
Perceived morality	3.21	0.68	2.98	0.72	$t(41) = 2.23$**, $p = 0.03$
Perceived gender	1.10	0.37	0.29	0.71	$t(41) = 11.54$**, $p < 0.001$
Perceived age	35.65[a]	5.24	36.86[a]	6.20	$t(36) = 1.38$, $p = 0.18$

For perceived gender, male is coded as 0, female as 1, and I do not know as 2. $N = 42$. [a]$N = 37$, *$p < 0.05$; **$p < 0.01$.

Measures

The survey was conducted in German. We used German translations or used a back-translation procedure (Brislin, 1970) to translate the scales into German. We adapted the scales using the gendered version of "supervisor" to increase gender salience. For each scale, items were presented in randomized order. If not stated differently, participants responded on a 7-point Likert scale (1 = *do not agree at all* to 7 = *totally agree*).

Perceived leader effectiveness

We measured perceived leader effectiveness (α = 0.96) with two items adapted from Gündemir et al. (2019, e.g., "This supervisor is a good leader.") and four items adapted from Rink et al. (2013, e.g., "This supervisor can instigate change.").

Perceived leader liking

Liking was operationalized using the nine-item scale of Montoya and Horton (2004), who adapted Byrne and Wong's (1962) Interpersonal Judgment Scale. We adapted the wording of the items to match the written scenario and to increase gender salience in German (e.g., "I would like to meet this supervisor."). We adapted the scale's general response range to a 7-point Likert scale (ranging for most items from 1 = *do not agree at all* to 7 = *entirely agree*; α = 0.97).

Perceived leader promotability

Promotability was assessed by three items (α = 0.90) adapted from Hentschel et al. (2018, e.g., "This supervisor should be recommended for a promotion.").

TABLE 2 English version of written scenarios for the manipulation.

Leadership behavior	
Servant leadership	Directive leadership
Your supervisor makes your career development a priority. *Your supervisor* emphasizes the importance of giving back to the community and puts the interests of *her/his* subordinates above *her/his* own. If you have a personal problem, you can seek help from *her/him*. *Your supervisor* recognizes when something work-related is going wrong. *Your supervisor* gives you the freedom to handle difficult situations in the way that you feel is best. *S/he* would *not* compromise ethical principles in order to achieve success.	*Your supervisor* lets you know what is expected of you. *Your supervisor* tells you what needs to be done and how it needs to be done. *Your supervisor* asks you to follow standard rules and regulations. *S/he* makes it clear to each of *her/his* subordinates what his or her role is in the group. *Your supervisor* explains the level of performance *s/he* expects from you. *S/he* would never give vague explanations about what is expected of you on the job.

The words that were gendered in the original German manipulation are highlighted in italics. The written manipulation of the leadership behavior was derived from the respective short scales of servant leadership (SL-7, Liden et al., 2015) and the five items for measuring directive leadership (Northouse, 2016). We created another item for the scenario about directive leadership to ensure an equal length of both leadership scenarios (e.g., "She makes it clear to each of her subordinates what his or her role is in the group."). The scenarios were written in German and equal in length, cues for leader gender, and cues addressing the reader. See Supplementary material (section #3.1) for the German scenarios.

Perceived leader prototypicality

Leader prototypicality was measured by four items (α = 0.94). Two items were adapted from Gündemir et al. (2019, e.g., "To what degree does this supervisor fit the image of a typical leader?"; 1 = *not very typical* to 7 = *very typical*). To include a behavioral component, we further added the items "To what degree does this supervisor act like a typical leader?" and "To what degree does this supervisor behave like a typical leader?" (1 = *not at all* to 7 = *entirely*).

we conducted all analyses with the smaller sample. The results of the hypotheses tests did not differ.

TABLE 3 Means and standard deviations of perceived servant leadership and directive leadership per condition.

	Servant leadership						Directive leadership					
	Woman leader			Man leader			Woman leader			Man leader		
	N	*M*	*SE*	*N*	*M*	*SE*	*N*	*M*	*SE*	*N*	*M*	*SE*
Perceived servant leadership	126	5.76	0.94	98	6.02	0.97	125	2.59	1.18	105	2.69	1.16
Perceived directive leadership		4.65	0.98		4.66	1.14		6.11	1.15		6.14	0.90

Ratings were given on a 7-point scale with higher scores indicating high levels of the respective variable.

TABLE 4 Means, standard deviations, and correlations of the dependent variables, mediators, and covariates.

		M	*SD*	1	2	3	4	5	6	7	8	9	10
1	Leader effectiveness	4.96	1.51										
2	Leader promotability	4.85	1.62	0.86**									
3	Leader liking	4.46	1.64	0.84**	0.85**								
4	Leader prototypicality	4.19	1.44	0.14**	−0.01	−0.06							
5	Leader warmth	3.28	1.19	0.66**	0.68**	0.78**	−0.23**						
6	Leader morality	3.68	0.99	0.75**	0.74**	0.79**	−0.06	0.85**					
7	Leader competence	3.74	0.91	0.73**	0.68**	0.65**	0.18**	0.61**	0.80**				
8	Leader dominance	2.61	1.13	−0.70**	−0.74**	−0.81**	0.23**	−0.82**	−0.75**	−0.50**			
9	Rater gender	0.50	0.50	0.10*	0.10*	0.09*	0.00	0.04	0.08	0.09	−0.07		
10	Rater age	45.92	11.66	−0.10*	−0.12*	−0.08	−0.04	−0.08	−0.11*	−0.10*	0.06	−0.22**	
11	Rater's managerial responsibility	0.27	0.44	−0.12**	−0.09	−0.04	−0.03	−0.04	−0.06	−0.12**	0.05	−0.11*	0.06

$N = 454$. Men are coded as 0, women are coded as 1. Age in years. Rater's managerial responsibility, no coded as 0, yes coded as 1. Leader liking refers to rater's perceived liking of the leader. *$p < 0.05$; **$p < 0.01$.

The facets of perceived leader warmth, morality, competence, and dominance

We operationalized the facets of perceived leader communion, *warmth* (α = 0.96) and *morality* (α = 0.92), as well as perceived leader agency, *competence* (α = 0.92) and, for the sake of completeness of this measurement tool, we also assessed for exploratory analyses another facet of agency, *assertiveness* (α = 0.82, see Supplementary material, section #3.2.1), by Abele et al.'s (2016) validated German scale. The scale comprised five items per facet. Responses to the question "The supervisor in the scenario seems to be …" were given on a bipolar five-point scale, with 5 indicating high levels of the respective facet.

We assessed *dominance* via the five items of the stereotype category dominance (Rosette et al., 2016, e.g., "bossy"). Participants responded to "The supervisor in the scenario seems to be …" on a 5-point Likert scale (1 = *do not agree at all* to 5 = *entirely agree*; α = 0.91; the item "demanding" was excluded as the corrected item-total correlation was below 0.30 and Cronbach's alpha was better when the item was deleted; Field, 2018).

Rater characteristics as control variables

Rater characteristics may influence the stereotypical perception of women and men. For *rater gender*, research found differences in the prevalence of gender stereotypes for female and male raters as well as men perceiving men in general to possess more leadership competence compared to women in general (Hentschel et al., 2019). Thus, male raters may perceive women leaders to score lower on competence compared to female raters. Similarly, *rater age* may influence the reaction toward women leaders and men leaders. Social role theory proposes that social roles change over time (Eagly and Wood, 2012) and research supports the change of gender stereotypes over time (Eagly et al., 2020). We controlled for rater age as older people potentially may hold more traditional gender role beliefs than younger people and may respond more negatively to a woman as a leader. Finally, we asked whether raters have *managerial responsibility* themselves as this might influence their leadership evaluation. Raters in supervisory roles may prefer their ingroup (leaders) over the outgroup (followers) due to in-group bias (*social identity theory*; Tajfel and Turner, 1986). Thus, they may rate other leaders more favorably. The results of our analyses did not differ when rerunning the analyses without these control variables (Becker et al., 2016; Bernerth and Aguinis, 2016).

Results

Table 4 depicts the correlations of all dependent variables, mediators, and the covariates. For the full correlation table including all demographics, please see the Supplementary material (section #3.2). Table 5 depicts the means and standard deviations of the dependent variables and mediators for each condition.[10]

10 We conducted a confirmatory factor analysis in *R* with *lavaan* to examine whether the measured variables represent distinct concepts. The results for our hypothesized 9-factor model suggest a good fit with the data, $\chi^2(1733, 454) = 4082.54$, $p < 0.001$, CFI = 0.92, TLI = 0.91, RMSEA = 0.06, SRMR = 0.06,

TABLE 5 Means and standard deviations of the dependent variables and mediators per condition.

	Servant leadership				Directive leadership			
	Woman leader[a]		Man leader[b]		Woman leader[c]		Man leader[d]	
	M	*SE*	*M*	*SE*	*M*	*SE*	*M*	*SE*
Leader effectiveness	5.72	0.97	5.80	1.11	4.12	1.49	4.28	1.52
Leader liking	5.49	0.92	5.59	1.12	3.36	1.42	3.49	1.49
Leader promotability	5.79	1.07	5.78	1.23	3.84	1.54	4.03	1.42
Leader prototypicality	3.81	1.30	3.46	1.44	4.70	1.31	4.73	1.32
Leader warmth	4.09	0.84	4.24	0.74	2.39	0.86	2.48	0.83
Leader morality	4.19	0.83	4.32	0.73	3.12	0.85	3.15	0.84
Leader competence	4.01	0.80	4.06	0.83	3.41	0.89	3.49	0.94
Leader dominance	1.80	0.75	1.72	0.66	3.46	0.83	3.39	0.82

Perceived leader effectiveness, promotability, liking, and prototypicality were rated on a 7-point Likert scale, while perceived leader warmth, morality, competence, and dominance were rated on a 5-point Likert scale. In both cases, higher scores indicate high levels of the respective variable. Leader liking refers to the rater's perceived liking of the leader. Means are adjusted for the covariates rater gender, rater age, and raters' managerial responsibility.

[a]$N = 126$.

[b]$N = 98$.

[c]$N = 125$.

[d]$N = 105$.

Test of gender-biased leader evaluation: effectiveness, liking, promotability, and prototypicality

To test H1 and H2,[11] we computed univariate analyses of covariance (ANCOVAs) in SPSS 27 to examine the main effects of the leadership behavior (coded as 0 = directive, 1 = servant), leader gender (coded as 0 = man, 1 = woman), and their interaction across the single dependent variables. As covariates, we included rater gender, rater age, and rater managerial responsibility.

> *H1*: Servant leadership compared to directive leadership relates more positively to perceived leader effectiveness (H1a), liking (H1b), and promotability (H1c) but less positively to perceived leader prototypicality (H1d).

Servant leaders received significantly higher ratings of perceived leader effectiveness ($F(1, 447) = 166.53$, $p < 0.001$, partial $\eta^2 = 0.27$), liking ($F(1, 447) = 319.92$, $p < 0.001$, partial $\eta^2 = 0.42$), and promotability ($F(1, 447) = 220.28$, $p < 0.001$, partial $\eta^2 = 0.33$) than directive leaders. In addition, we computed pairwise comparisons due to heterogeneity of cell variances indicated by Levene's test and used the robust method bootstrapping (1,000 resamples, Field, 2018). Pairwise comparisons revealed that servant leaders were perceived as more effective ($M_{SL} = 5.76$, $M_{DL} = 4.21$, 95% CI [1.32, 1.79], $p < 0.01$), more likable ($M_{SL} = 5.54$, $M_{DL} = 3.43$, 95% CI [1.90, 2.32], $p < 0.01$), and more promotable ($M_{SL} = 5.78$, $M_{DL} = 3.94$, 95% CI [1.58, 2.07], $p < 0.01$) than directive leaders.[12] For perceived leader prototypicality, no further analyses were computed.[13] H1a to H1c were supported as we found a main effect of leadership behavior on leader effectiveness, liking, and leader promotability.

> *H2*: For men (women) leaders as compared to women (men) leaders, servant (directive) leadership relates more positively to perceived leader effectiveness (H2a), liking (H2b), and promotability (H2c) but less positively to perceived leader prototypicality (H2d).

compared to a single factor model, $\chi^2(1769, 454) = 13900.92$, $p < 0.001$, CFI = 0.57, TLI = 0.55, RMSEA = 0.12, SRMR = 0.15, $\Delta\chi^2(36) = 9818.38$, $p < 0.001$. An eight-factor model merging perceived warmth and morality into the factor communion, $\chi^2(1741, 454) = 4453.30$, $p < 0.001$, CFI = 0.90, TLI = 0.90, RMSEA = 0.06, SRMR = 0.06, $\Delta\chi^2(8) = 370.77$, $p < 0.001$, as well as a seven-factor model merging perceived competence and dominance into the factor agency, $\chi^2(1748, 454) = 5579.64$, $p < 0.001$, CFI = 0.86, TLI = 0.86, RMSEA = 0.07, SRMR = 0.07, $\Delta\chi^2(15) = 1497.10$, $p < 0.001$, showed a worse fit with the data.

11 Before testing H1, we conducted a multivariate analysis of covariance (MANCOVA) to test the effects of the leadership behavior, leader gender, and their interaction on all four dependent variables including the covariates. The MANCOVA revealed a statistically significant difference between the leadership behaviors on the dependent variables, $F(4, 444) = 128.49$, $p < 0.001$, partial $\eta^2 = 0.54$, Wilk's $\Lambda = 0.46$. However, we found no significant main effect of leader gender, $F(4, 444) = 1.45$, $p = 0.22$, partial $\eta^2 = 0.01$, Wilk's $\Lambda = 0.99$, and no significant interaction effect between leadership behavior and leader gender on the combined dependent variables, $F(4, 444) = 0.79$, $p = 0.53$, partial $\eta^2 = 0.01$, Wilk's $\Lambda = 0.99$.

12 The residuals of perceived leader effectiveness and liking were normally distributed, as determined by the Shapiro–Wilk test, ($p > 0.05$). The residuals of perceived leader promotability were normally distributed when assessed by the Kolmogorov–Smirnov test, ($p > 0.05$), but they were not normally distributed as determined by the stricter Shapiro–Wilk test ($p = 0.03$). This is another reason why we conducted bootstrapping.

13 For perceived leader prototypicality the homogeneity of regression slopes was violated for the interaction term of the independent variable leadership behavior and the covariate rater gender, as the interaction terms were statistically significant ($p < 0.05$).

We found no significant main effect of leader gender indicating women and men were not evaluated differently on perceived leader effectiveness ($F(1, 447) = 1.91$, $p = 0.17$, partial $\eta^2 = 0.00$), liking ($F(1, 447) = 1.44$, $p = 0.23$, partial $\eta^2 = 0.00$), and promotability ($F(1, 447) = 1.11$, $p = 0.29$, partial $\eta^2 = 0.00$). We also found no interaction effect of leadership behavior and leader gender on perceived leader effectiveness ($F(1, 447) = 0.06$, $p = 0.80$, partial $\eta^2 = 0.00$), liking ($F(1, 447) = 0.01$, $p = 0.93$, partial $\eta^2 = 0.00$), and promotability ($F(1, 447) = 0.40$, $p = 0.53$, partial $\eta^2 = 0.00$) indicating that women and men were not evaluated differently for exhibiting either servant or directive leadership. Thus, H2 was not supported.

Test of moderated mediation: warmth, morality, competence, and dominance as mediators

> *H3*: Servant (compared to directive) leadership positively relates to perceptions of leader warmth (H3a) and morality (H3b), which, in turn, positively relate to perceived leader effectiveness and liking, and, ultimately, to promotability. These mediation effects are stronger for men leaders compared to women leaders.
>
> *H4*: Servant (compared to directive) leadership positively relates to perceptions of leader competence (H4a) and negatively relates to perceptions of leader dominance (H4b). In turn, competence positively and dominance negatively relate to perceived leader effectiveness and liking, and, ultimately, to promotability. These mediation effects are stronger for women leaders compared to men leaders.

To test H3 to H4, we used the PROCESS macro, version 4.2 (Hayes, 2018) in SPSS 27 to compute all moderated mediation analyses. We tested hypotheses using bootstrapping (5,000 resamples) with 95% bias-corrected confidence intervals of the hypothesized indirect effects. The same covariates were used. As independent variable, we included leadership behavior. The moderator variable was leader gender. To test the serial moderated mediation model of H3 through H4, we implemented model 83, with either perceived leader warmth, morality, competence, or dominance as first mediator and either perceived leader effectiveness or liking as second mediator, and perceived leader promotability as dependent variable. We z-standardized all continuous variables to account for the different scale ranges of the mediators.

For H3 to H4, we found support for the proposed positive indirect effect of leadership behavior on perceived leader promotability via perceived warmth (H3a), morality (H3b), competence (H4a) and for the proposed negative indirect effect via perceived dominance (H4b) for women and men leaders via perceived leader effectiveness and liking (see Table 6 for the indirect effects, see the Supplementary material for the PROCESS output of each serial moderated mediation, Supplementary material, section #3.2). Leadership behavior positively predicted perceived warmth ($B = 1.49$, $SE = 0.09$, 95% CI [1.31;1.66]), morality ($B = 1.20$, $SE = 0.11$, 95% CI [0.98; 1.41]), competence ($B = 0.62$, $SE = 0.13$, 95% CI [0.36; 0.89]), and negatively predicted perceived dominance ($B = -1.47$, $SE = 0.09$, 95% CI [−1.66; −1.29]). Warmth positively predicted effectiveness ($B = 0.59$, $SE = 0.07$, 95% CI [0.46; 0.72]) and liking ($B = 0.65$, $SE = 0.06$, 95% CI [0.53; 0.79]) which positively predicted leader promotability (effectiveness: $B = 0.71$, $SE = 0.04$, 95% CI [0.64; 0.79]; liking: $B = 0.81$, $SE = 0.05$, 95% CI [0.72; 0.90]). Morality positively predicted effectiveness ($B = 0.66$, $SE = 0.06$, 95% CI [0.54; 0.78]) and liking ($B = 0.62$, $SE = 0.05$, 95% CI [0.52; 0.73]) which positively predicted leader promotability (effectiveness: $B = 0.66$, $SE = 0.04$, 95% CI [0.58; 0.74]; liking: $B = 0.71$, $SE = 0.05$, 95% CI [0.60; 0.81]). Competence positively predicted effectiveness ($B = 0.62$, $SE = 0.05$, 95% CI [0.52; 0.72]) and liking ($B = 0.49$, $SE = 0.04$, 95% CI [0.41; 0.57]) which positively predicted leader promotability (effectiveness: $B = 0.66$, $SE = 0.04$, 95% CI [0.58; 0.74]; liking: $B = 0.65$, $SE = 0.05$, 95% CI [0.56; 0.74]). Dominance negatively predicted effectiveness ($B = -0.66$, $SE = 0.06$, 95% CI [−0.78; −0.55]) and liking ($B = -0.72$, $SE = 0.05$, 95% CI [−0.81; −0.63]) which positively predicted leader promotability (effectiveness: $B = 0.66$, $SE = 0.04$, 95% CI [0.58; 0.74]; liking: $B = 0.74$, $SE = 0.05$, 95% CI [0.64, 0.83]). Yet, the bootstrapping confidence intervals of the index of the moderated mediation included zero, which indicates that indirect effects did not differ according to leader gender (see Table 6 for the respective results).[14] Thus, H3 to H4 were only partially supported.

Discussion

Leadership behavior matters for the evaluation of leaders and leaders' careers. In this paper, we showed that servant and directive leadership are related to leaders' promotability. In our study, servant leaders were perceived as more effective and likable, and thus ultimately more promotable than directive leaders. We examined the underlying mechanisms of this relationship. The facets of the leader's perceived communion and agency explained the relationship between leadership behavior and these serial outcomes. Specifically, we found a *positive* relationship of servant (vs. directive) leadership with perceived leader effectiveness and liking. Servant leadership related to more effectiveness and liking via higher warmth, morality, and competence perceptions as well as via lower dominance perceptions. Warmth, morality, and competence positively related, whereas dominance negatively related to leader

14 As additional analyses we computed ANCOVAs to examine the main effects of leadership behavior and leader gender and their interaction on the facets of communion and agency. Results revealed that servant leaders compared to directive leaders received significantly higher ratings of warmth ($F(1, 447) = 498.88$, $p < 0.001$, partial $\eta^2 = 0.53$), morality ($F(1, 447) = 210.70$, $p < 0.001$, partial $\eta^2 = 0.32$), competence ($F(1, 447) = 50.57$, $p < 0.001$, partial $\eta^2 = 0.10$), and lower ratings of dominance ($F(1, 447) = 523.49$, $p < 0.001$, partial $\eta^2 = 0.54$). We computed pairwise comparisons and used the robust method bootstrapping (1,000 resamples, Field, 2018). Pairwise comparisons revealed that servant leaders were perceived as warmer ($M_{SL} = 4.17$, $M_{DL} = 2.44$, 95% CI [1.58, 1.88], $p < 0.01$), more moral ($M_{SL} = 4.25$, $M_{DL} = 3.14$, 95% CI [0.97, 1.26], $p < 0.01$), more competent ($M_{SL} = 4.03$, $M_{DL} = 3.46$, 95% CI [0.42, 0.73], $p < 0.01$) and less dominant ($M_{SL} = 1.76$, $M_{DL} = 3.42$, 95% CI [−1.82, −1.53], $p < 0.01$) than directive leaders. We again found no main effect for leader gender and no interaction effect between leadership behavior and leader gender.

TABLE 6 Indirect effects and index of the moderated serial mediation for H3 to H4.

Condition	Predictor	1st Mediator	2nd Mediator	Outcome	Path	*B*	*SE*	*95% CI*
Woman	Leadership behavior	Warmth	Effectiveness	Promotability	X→M1→M2→O	0.60	0.09	[0.44, 0.79]
Man	Leadership behavior	Warmth	Effectiveness	Promotability	X→M1→M2→O	0.63	0.09	[0.47, 0.80]
Index of moderated mediation						−0.03	0.05	[−0.13, 0.08]
Woman	Leadership behavior	Warmth	Liking	Promotability	X→M1→M2→O	0.75	0.10	[0.56, 0.97]
Man	Leadership behavior	Warmth	Liking	Promotability	X→M1→M2→O	0.79	0.10	[0.61, 1.00]
Index of moderated mediation						−0.04	0.07	[−0.17, 0.10]
Woman	Leadership behavior	Morality	Effectiveness	Promotability	X→M1→M2→O	0.46	0.08	[0.33, 0.63]
Man	Leadership behavior	Morality	Effectiveness	Promotability	X→M1→M2→O	0.52	0.07	[0.40, 0.67]
Index of moderated mediation						−0.06	0.07	[−0.19, 0.08]
Woman	Leadership behavior	Morality	Liking	Promotability	X→M1→M2→O	0.47	0.07	[0.34, 0.61]
Man	Leadership behavior	Morality	Liking	Promotability	X→M1→M2→O	0.53	0.07	[0.40, 0.67]
Index of moderated mediation						−0.06	0.07	[−0.19, 0.08]
Woman	Leadership behavior	Competence	Effectiveness	Promotability	X→M1→M2→O	0.26	0.06	[0.16, 0.38]
Man	Leadership behavior	Competence	Effectiveness	Promotability	X→M1→M2→O	0.26	0.06	[0.14, 0.37]
Index of moderated mediation:						0.01	0.07	[−0.13, 0.15]
Woman	Leadership behavior	Competence	Liking	Promotability	X→M1→M2→O	0.20	0.04	[0.12, 0.30]
Man	Leadership behavior	Competence	Liking	Promotability	X→M1→M2→O	0.20	0.05	[0.11, 0.29]
Index of moderated mediation						0.01	0.06	[−0.11, 0.12]
Woman	Leadership behavior	Dominance	Effectiveness	Promotability	X→M1→M2→O	0.64	0.08	[0.49, 0.81]
Man	Leadership behavior	Dominance	Effectiveness	Promotability	X→M1→M2→O	0.64	0.08	[0.50, 0.81]
Index of moderated mediation						−0.01	0.06	[−0.11, 0.11]
Woman	Leadership behavior	Dominance	Liking	Promotability	X→M1→M2→O	0.77	0.09	[0.62, 0.96]
Man	Leadership behavior	Dominance	Liking	Promotability	X→M1→M2→O	0.78	0.09	[0.62, 0.96]
Index of moderated mediation						−0.01	0.07	[−0.14, 0.12]

$N = 454$. The moderated mediations included the covariates rater age, rater gender, and raters' managerial responsibility. The indirect effects and the index of the moderated mediation were computed using bootstrapping (5,000 resamples).

promotability via perceived leader effectiveness and liking. We also examined whether leader gender biases the evaluations of servant and directive leadership. As our results show, servant leadership was indeed more expected of women leaders. However, directive leadership was expected of women leaders and men leaders alike. This supports recent findings that an agentic leadership behavior is equally expected of both genders, while more communal leadership behavior is more expected of women (Hentschel et al., 2018). Contrary to our expectations, our results indicate no gender-biased evaluations of servant or directive leadership. Both women and men were perceived as equally communal and agentic for the same leadership behavior.

Theoretical implications

Our results have implications for research on leader promotability regarding servant and directive leadership. We found that servant leaders were perceived as more effective, likable, and promotable than directive leaders, which aligns with previous research highlighting numerous positive outcomes of servant leadership for organizations and followers (Hoch et al., 2018; Eva et al., 2019; Lee et al., 2020). Up to now, it remained unclear whether servant leadership also serves leaders themselves. Our research provides evidence that also leaders themselves benefit from servant leadership. So far, servant leadership has been shown to be effective across cultures (Pekerti and Sendjaya, 2010; Zhang et al., 2021). We provide evidence that servant leadership is universally effective concerning gender as its evaluation does not vary depending on leader gender. In other words, servant leadership seems to benefit the careers of women and men alike.

Our research also highlights the relevance of examining gender-biased evaluations for each leadership behavior. We found no evaluative bonus or penalty for servant and directive leadership. Yet, research on other communal and agentic behaviors has at least partly demonstrated a bonus or penalty (e.g., Rudman et al., 2012; Hentschel et al., 2018). It could thus be misleading to generalize from one communal or agentic leadership behavior onto another. Regarding directive leadership, our findings are consistent with expectancy-violation theory (Jussim et al., 1987; Prentice and Carranza, 2004). Since directive leadership was equally expected of women and men, directive women leaders and directive men leaders received equal evaluations. This aligns with previous research showing no gender differences in expectation and evaluation of autocratic leadership, another agentic yet more strongly domineering leadership behavior (Hentschel et al., 2018). Our findings also resonate with research that women need to exhibit agency to prove that they have leadership qualities (Johnson et al., 2008; Bongiorno et al., 2014). According to our findings, directive women leaders seem to meet this agency expectation. Thus, they might have been perceived to own the same leadership abilities as men leaders.

An alternative explanation for our findings may be the selected leadership behaviors. Servant leaders were perceived to display a certain level of directive leadership. Raters may have assumed that servant leaders, by default, provide a certain degree of guidance and direction to followers, the minimal requirements for good leadership. Women and men showing directive leadership might have just been perceived as fulfilling the typical leader role. Consistently, according to the mean values across our four conditions, directive leaders were deemed as more prototypical than servant leaders. In contrast to directive leaders, servant leaders might have been perceived as exceptional leaders. They may have been assumed to exhibit the behaviors of directive leadership augmented by servant leadership. In this regard, servant leaders might positively violate expectations how leaders typically are and thus receive an evaluative bonus in line with expectancy-violation theory (Prentice and Carranza, 2004).

Even though servant leadership was expected more of women than of men, servant men leaders were not evaluated more favorably. This seems to contradict expectancy-violation theory (Prentice and Carranza, 2004). Yet, two different violations might have occurred for which this theory does not account. In its original conception, expectancy-violation theory focused on personal space violations (Burgoon, 1978, 2015). These could either be perceived as positive, resulting in a bonus, or as negative, resulting in a penalty. But leadership behavior may involve positive and negative violations at the same time. Servant men leaders may have gained no communion bonus due to a penalty for lacking dominance. Indeed, we found servant leaders to be perceived as low on dominance. The penalty for this dominance deficit may be evident in a devaluation of men. Servant leaders put their followers first and support others' careers instead of their own career. Hence, servant men leaders might seem to violate prescriptions that men should be competitive and dominant (see also Prentice and Carranza, 2002; Rudman et al., 2012). As dominance is linked to status, men (but not women) who lack dominance seem to violate the gender hierarchy (for a discussion, see Moss-Racusin et al., 2010; Rudman et al., 2012). This aligns with previous research that found no bonus for servant men leaders related to follower outcomes (Lemoine and Blum, 2021). Our reasoning could also explain why men receive a communion bonus for transformational leadership (Hentschel et al., 2018). Instead of putting followers first, transformational leadership focuses on reaching organizational goals (Stone et al., 2004) and may not violate men's dominance prescriptions. Concluding, the communion bonus for servant men leaders may have been obscured by a dominance deficit.

Our research further adds knowledge on the mechanisms underlying the evaluation of servant and directive leadership. We established a mediating role of perceived leader communion (i.e., warmth, morality) and agency (i.e., competence, dominance). Interestingly, our results do not align with shifting standards theory (Biernat, 2012). Women and men were perceived to score equally on communion and agency for the same leadership behavior and there was no gender-biased evaluation. Instead, our findings align with newer research suggesting competence to be perceived as equally characteristic of both genders (Hentschel et al., 2019; Eagly et al., 2020).

Focusing on the facets of communion and agency, our results underline the need to distinguish competence and dominance as subdimensions of agency (Rosette et al., 2016). Perceived leader competence was positively, and perceived leader dominance negatively, related to perceived leader effectiveness, liking, and promotability. Regarding the content of both agentic dimensions, competence seems to be socially desirable, whereas dominance is generally deemed undesirable (Prentice and Carranza, 2002; Ma et al., 2022).

Managerial implications

Our results provide rich implications for managers and organizations that want to promote effective leadership behaviors, leaders' careers, and gender equality. As our findings suggest, servant leaders are perceived as more effective, likable, and promotable compared to directive leaders. Thus, servant leadership holds benefits for leaders beyond the positive outcomes shown for organizations and followers (e.g., Hoch et al., 2018). Hence, leaders may be more motivated to show servant leadership if this leadership behavior also serves their careers. Importantly, women and men servant leaders profited equally from servant leadership. Thus, organizations are well-advised to provide leadership training on how to become a servant leader (e.g., training mindfulness; Pircher Verdorfer, 2016) to establish effective leadership behaviors and to advance women in leadership. Consistent with findings on the more important role of structural than individual adjustments (Gloor et al., 2020), servant leadership should be seen as a steppingstone on the way to changing the system toward gender equality. It would be short-sighted to promote servant leadership as a general cure to women's underrepresentation or disadvantage in leadership.

Our findings offer recommendations for leaders on how to be seen as more effective and likable. In this regard, leaders benefit from being perceived as competent, warm, or moral. Being perceived as dominant harms their perceived leader effectiveness, liking, and thus their promotability. Hence, leaders are generally well advised to display competence, warmth, and morality and avoid dominant behaviors.

Limitations and future research

Despite its contributions, our research holds several limitations. First, we implemented a fictional business case scenario in an online experimental environment rather than examining the evaluation of real supervisors' leadership behavior. We used the conditions of the scenarios as independent variables and assumed that women and men who exhibit the same behavior are perceived as equally exhibiting servant leadership or directive leadership. The dependent variables were assessed by raters who were supposed to imagine being supervised by the depicted leader. Yet, the supervised followers seldom have a say in who is promoted in the organization. Moreover, our scenario contained no competitive context where raters could decide on whether either a woman or a man showing the same leadership behavior should be promoted as leader. Future research may examine the proposed relationships in the workplace and test the gender-biased evaluation of other leadership behaviors. This may also be conducted with raters as promotion committee members and in the field.

Second, we examined the evaluation of a formal supervisor. Raters might have been biased as the supervisor was assigned to her/his position with formal power instead of claiming the leader role herself/himself (see DeRue and Ashford, 2010). Claiming the leadership role might evoke perceptions of a will to lead. Claiming the leadership role might have a gendered impact on the leader's perceived promotability as self-promoting harms women's likability but not men's (e.g., Rudman and Glick, 2001). On the other hand, if women leaders are granted the position of the leader by others, this might increase perceptions of their leadership competence. Thus, results might differ for a scenario about an informal or self-chosen leader.

Finally, we did not account for the intersectionality of gender and other discrimination variables like for example ethnicity or age via the provided silhouettes. Raters had probably primarily thought about White leaders as White people prevail in Western societies' leadership positions (Alliance for Board Diversity Census, 2021). Nevertheless, these limitations hold options for future research. Due to the intersection of gender and ethnic stereotypes (e.g., Rosette et al., 2016), Asian women are stereotyped as very feminine and passive (Galinsky et al., 2013; Rosette et al., 2016), while Black men are stereotyped as very masculine and threatening (e.g., Galinsky et al., 2013; Todd et al., 2016). Thus, directive leadership may provide an agency bonus for Asian women leaders and servant leadership may provide a communion bonus for Black men leaders compared to their ethnic counterparts. Age might also play a significant role. Our silhouettes were rated as belonging to adults in their mid-thirties.[15] Younger leaders are seen as less effective and likable compared to middle-aged leaders and leader age can even overshadow gender information (Daldrop et al., 2023). It remains to be seen whether younger leaders profit more from implementing servant leadership compared to middle-aged leaders thanks to a communion bonus, or whether they suffer due to losing status (see Buengeler et al., 2016). Despite being universally effective across cultures (Pekerti and Sendjaya, 2010), servant women leaders and servant men leaders could receive differing evaluations depending on the local culture, gender expectations, and strictness of gender roles (e.g., gender egalitarianism, House et al., 2004). Hence, it would be interesting to examine the leadership evaluations with raters' individual cultural orientations as moderators.

For future research on expectancy violation, we encourage to first examine whether the expectations for a certain leadership behavior are biased. If the same leadership behavior for example is expected of women and men, then no expectancy violation and no evaluative bias can occur. Thus, we welcome research regarding gender-biased and intersectional leader prototypes of women leaders and men leaders. In addition, the valence (positive vs. negative) of the respective behavior should also be examined. Based on the valence, one can conclude whether an expectancy violation is perceived as positive or negative, resulting in either bonus or penalty.

Future research should further examine which role a leader's perceived communion and agency play in promotion decisions. A person's perceived communion contributes more to forming a first overall judgment than a person's perceived agency, but the importance of agency increases with increasing outcome dependency (Abele and Wojciszke, 2007). Thus, a leader's communion and agency may play a pivotal role in leadership evaluations as well as in resulting promotion decisions, depending on how well the promotion committee knows the leader. Future research should address this relationship and the role of rater's perceived outcome dependency which rater's gender stereotypes could influence.

Despite servant leadership's seeming gender-neutral evaluation, we encourage future research regarding the interplay with leader gender. For example, Eva et al. (2019) suggested examining whether leaders are negatively influenced by exhibiting servant leadership as evident in higher stress or burn-out. Women leaders could have

15 Interestingly, servant leaders were perceived as younger than directive leaders (see Supplementary material, section #3.2).

higher emotional costs for displaying servant leadership than men because they still primarily fulfill the role of a "servant" in house- and care-work. Due to gender roles of women as caretakers, women might receive less appreciation for displaying servant leadership compared to men. This lower appreciation would reduce the resources that servant leaders gain from helping their followers, as appreciation seems to compensate for the resources lost by showing servant leadership (Xu and Wang, 2018). If women leaders are not internally motivated to practice servant leadership but receive external pressure to do so, they will likely suffer physically and psychologically (Vial and Cowgill, 2022). Thus, it will be important to examine potential gender differences in servant leadership's effects on leaders.

Conclusion

In this paper, we examined whether leaders themselves profit more from implementing servant or directive leadership behavior – and if leader gender plays a role in this. Our research suggests that servant leaders are perceived to be more effective, likable, and promotable than directive leaders, regardless of leader gender. Being seen as warm, moral, and competent is positively, and being seen as dominant is negatively, related to perceived leader effectiveness, liking, and thus promotability. Leadership behaviors are key to leadership development and strategies to empower aspiring (women) leaders. As servant leadership seems to be gender-neutral in its evaluation, we suggest servant leadership as a leadership behavior that serves not only organizations and followers but also benefits leaders' careers.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

AB primarily developed, designed, and analyzed the study and wrote the first draft. CB contributed to all steps of the process. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2023.957121/full#supplementary-material

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I am one of you! Team prototypicality as a facilitator for female leaders

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In the present study, we complement role congruity theory with insights from the Social Identity Model of Leadership. We propose that especially female leaders benefit from team prototypicality, i.e., being representative of the group they are leading. We assume that team prototypicality shifts the comparative frame away from higher-order categories like gender and leader roles to more concrete team-related properties and thereby reduces disadvantages for female leader that stem from the incongruity between the leader role and the female gender role stereotypes. Further, this effect should affect both (female) leaders themselves and their perception by their followers. Building on previous research, we predict, first, lower authentic leadership behavior for female than male leaders. Second, that team prototypicality positively relates to authentic leadership and trust in leader. Third, that team prototypicality has stronger relations to authentic leadership and trust in leader for female compared to male leaders. We tested assumptions in a randomized online experiment (Study 1, N=315) and a cross-sectional survey study (Study 2, N=300). We did not find consistent support for the assumed gender differences in authentic leadership. But our results (both in manifest and in latent analyses) show that team prototypicality—both self-perceived (Study 1) and as perceived by employees (Study 2)—is related to more authentic leadership and more trust in leader (Study 2) and that these relations are stronger for female than for male leaders. Furthermore, we tested in Study 2 an extended model including follower's job satisfaction as the final follower outcome affected *via* team prototypicality, leader gender, authentic leadership, and trust in leader. Thereby, we found that team prototypicality has direct and indirect effects on job satisfaction as carried through authentic leadership and trust in leader, respectively. Together, the results of both studies support our assumptions and show that female leaders can reduce role incongruity barriers through high team prototypicality. Implications for future research and practical implications of these results for gender equality are discussed.

KEYWORDS

Prototypicality, authentic leadership, social identity model of leadership, gender roles, gender stereotypes, team prototypicality

Introduction

Women constitute almost half of today's workforce worldwide (The World Bank, 2020), and yet, women are still under-represented in upper echelons of most FT-500 firms (Catalyst, 2021). Such under-representation has persisted for decades, even after organizations started implementing gender equality policies and quotas to help women reach and maintain leadership positions. While reasons why women struggle to emerge as and be successful leaders have been explained elsewhere (e.g., Eagly and Karau, 2002; Ryan and Haslam, 2007), these figures suggest that there is still a need for new insights that can contribute to the reduction of discrimination and prejudice women experience once they made it into a leadership position, and thus, facilitate their exercise of leadership.

From a psychological perspective, Role Congruity Theory (RCT; Eagly and Karau, 2002) captures the prevailing scholarly consensus on why women suffer a double bind and prejudice well. In short, RCT's core proposition is that traditional gender and leader role stereotypes tend to align for men (or those who identify with the male gender), but not for women (or those who identify with the female gender). For almost two decades, empirical research has supported RCT's claims about the mechanics of discrimination and prejudice toward women in leadership roles (Heilman, 2012; Hernandez Bark et al., 2014; Badura et al., 2018; Manzi and Heilman, 2021).

However, while RCT provides a good conceptual framework for the understanding of the mechanisms behind discrimination that female leaders are exposed to, the reports by both the World Bank and Catalyst suggest that the insights of RCT did not contribute to change the underrepresentation of women in higher leadership in contemporary firms. Thus, female leaders might benefit from additional empirical insights that can extend or complement RCT while honoring its core propositions. For example, a recent study extended RCT theory to the field of entrepreneurship, attempting to find ways to reduce the societal pressures that elicit antisocial behaviors in female leaders and entrepreneurs (Monzani et al., 2021). In the present study, we propose complementing RCT with insights from the Social Identity Model of Leadership (SIMOL; Hogg, 2001).

Following the claims of SIMOL theory, prototypicality, and especially team prototypicality, would allow female leaders to tackle some of the barriers resulting from role incongruity. Therefore, the main objective of the present study is to test if the propositions of SIMOL could complement the insights provided by Role Congruity Theory in order to support female leaders. More precisely, we inquire if prototypicality enables women to perceive themselves and be perceived by others as effective leaders (van Knippenberg et al., 2004; Van Dick and Kerschreiter, 2016). More precisely, we focus on leveraging prototypicality when leading a workgroup. Prototypicality means that the leader is perceived as "one of us," as a model member of the team, or ideally as "the best of us" (meaning as an exemplary member of the team; Van Dick and Kerschreiter, 2016). We believe that team prototypicality, thus being representative of the team one is leading, would help female leaders overcome the obstacles and prejudice resulting from the mismatch between the female gender role stereotype (communal) and the leadership role stereotype (agentic) still prevailing in contemporary organizations. If our predictions were to be supported by our data, our work would make valuable theoretical and empirical contributions to RCT, SIMOL, and its recent extension, Identity Leadership (Haslam et al., 2021). More precisely, by shifting the focus from battling rigid societal stereotypes to managing the identity dynamics of the groups they lead, women can transcend the role incongruity described by RCT and be more effective in attaining and sustaining leadership positions, but also feel more self-expressive when occupying said positions.

The core premise of our study is grounded on extant evidence, which suggests that leveraging a prototypical status might be a valuable tool to enhance female leadership. For example, followers of prototypical leaders tend to be more tolerant when their leaders fail to achieve goals (Giessner and van Knippenberg, 2008). Similarly, followers are also more tolerant when leaders breach existing social norms, such as ensuring procedural justice (Ullrich et al., 2009). Thus, in the present study, we propose that being perceived as "one of us in the work team," so especially the team prototypical status, is one possibility for female leaders to overcome role incongruity issues – both for themselves and in the perception of their followers – and to increase their authentic leadership behavior as well as their employee's trust in them. Team prototypicality focuses on both the team itself and its leader being representative for the team. We assume that such focus shifts the comparative dimension from higher-order categories like leader or gender to more concrete, team-related categories and thereby allows women to overcome problems emerging from role incongruity. Figure 1 illustrates our proposed core model.

Theoretical framework

Leadership, understood as a social influence process, does not occur in a social vacuum, but is enacted in social groups. In organizational settings, extant theory on social categorization suggests that social groups (e.g., teams) tend to construct shared representations of what constitutes the ideal characteristics and

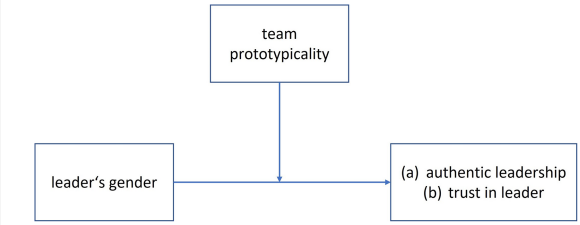

FIGURE 1
Proposed core model.

behaviors that would describe someone belonging to said group, or what is known as a group's *prototype* (Hogg and Terry, 2000). Unless leaders actively engage in identity entrepreneurship to (re) shape their group's prototype (Steffens et al., 2014; van Dick et al., 2018), said prototype will likely be based on the prevailing role stereotypes of the society or culture in which the firm operates. Therefore, we theorize briefly the interplay between gender and leader roles within organizations.

Gender and leadership

Gender stereotypes consist of descriptive, prescriptive, and proscriptive components (Eagly et al., 1995; Eagly and Karau, 2002; Cuddy et al., 2008; Rudman et al., 2012). In other words, gender stereotypes shape societal expectations on how women and men actually behave (descriptive), but also on how they should (prescriptive) and should not behave (proscriptive). Women are usually expected to display communal attributes and behaviors whereas men are usually expected to display agentic attributes and behaviors. The female gender role stereotype is associated with being concerned about the well-being of others and thereby with communal attributes such as being warm, kind, friendly, empathic, supportive, gentle, and caring (Bakan, 1966; Eagly, 1987; Williams and Best, 1990; Abele et al., 2008; Rudman et al., 2012; Hernandez Bark et al., 2014; March et al., 2016). In contrast, the male role stereotype is associated with agentic attributes such as being self-confident, ambitious, assertive, controlling, independent, dominant, and competitive (Bakan, 1966; Eagly, 1987; Williams and Best, 1990; Abele et al., 2008; Rudman et al., 2012; Hernandez Bark et al., 2014; March et al., 2016). Despite some changes, especially in the female gender stereotype, the general pattern of men being more closely associated with agentic properties and women being more closely associated with communal properties was confirmed by various research (Hentschel et al., 2019; Obioma et al., 2021) and two recent meta-analyses (Eagly et al., 2020; Hsu et al., 2021).

Schein (1973) already proposed the *think manager—think male paradigm* indicating that leader stereotypes are associated with male connotated properties. In their meta-analysis, Koenig et al. (2011) included in addition to Schein's think manager—think male paradigm, also the *agency–communion paradigm* (Powell and Butterfield, 1979) and the *masculinity-femininity paradigm* (Shinar, 1975) to examine leader stereotype content. They found that leader stereotypes are more closely associated with males, agency, and masculinity. Thus, independent of the underlying paradigm, leadership stereotypes are more closely associated with men than with women. Although this pattern slightly decreased over time, it is still valid nowadays and to be found in recent research (Hoyt et al., 2011; Badura et al., 2018; Heilman and Caleo, 2018).

According to role theory (Biddle, 1979), conforming with social role prescriptions is one fundamental criterion for the perception and evaluation of an individual in a given social group or context, such as an organization. For example, in modern organizations, job roles describe the specific characteristics that an employee should possess to occupy such role (descriptive), and the performance expectations for those who occupy such roles (prescriptive). Similarly, most organizations have social norms and policies to address deviations from a job role prescription (proscriptive). In most organizations, managerial positions confirm with the agentic connotated "leader" role stereotype, which in turn has unfortunate implications for women in leadership roles, as RCT suggests.

RCT's core proposition states that the traditional, prevailing gender and leader role stereotypes tend to align better for men than for women (Eagly and Karau, 2002; Heilman, 2012; Hernandez Bark et al., 2014). This incongruity between the traditional female and leader role stereotypes creates a double standard (female leaders must perform better than their male counterparts to be perceived as competent) and a double bind (to be "tough" and "nice" at the same time; Eagly and Karau, 2002). Thus, women have to overcome various obstacles on their way to leadership positions, such as perceiving managerial positions as less attractive (reduced leadership aspirations) and reduced authenticity when occupying leadership roles (Eagly, 2005; Eagly and Carli, 2007; Heilman, 2012; Hernandez Bark et al., 2014; Monzani et al., 2014).

Unfortunately, in organizational settings, gender role stereotypes tend to facilitate biases, prejudice, and discrimination against those individuals that seek roles that do not align with their stereotypical gender roles (Konrad et al., 2000; Rudman and Glick, 2001; Schein, 2001; Eagly and Karau, 2002; Eagly, 2005; Koenig et al., 2011; Heilman, 2012; Rudman et al., 2012; Hernandez Bark et al., 2014, 2016, 2021; Koch et al., 2015; Hernandez Bark et al., 2022; Junker et al., 2022). For example, regarding stereotypical biases based on gender roles, women are more closely associated with the stereotype of followers (the think follower—think female paradigm, Braun et al., 2017), and men are more closely associated with the stereotype of leaders (*think manager—think male* paradigm; Schein, 2001). Thus, women and other equity-deserving groups frequently struggle to occupy leadership roles. Despite some changes, the *think manager—think male* phenomenon still prevails. In this context, the *think manager–think male*, captures the mental picture of a typical leader containing more masculine attributes and being more strongly associated with the male gender stereotype (Schein, 2001; Koenig et al., 2011). Thus, employees operating under a female leader tend to experience cognitive dissonance due to the incongruity between the stereotypical attributes desired of women and the requirements of a leadership role. This dissonance affects both women's self-perception and their perception by others (Heilman, 2001, 2012; Horvath and Sczesny, 2016).

The prejudice that female leaders suffer from creates substantive drawbacks for women in organizations. For example, women are ascribed less leadership potential and are evaluated less favorably in leadership positions (Heilman, 2001, 2012; Eagly and Karau, 2002; Lord and Hall, 2003). One well-known

possibility for female leaders to reduce this incongruity is to embrace a transformational leadership style, as its facets include communal behaviors (e.g., showing individual consideration for their followers). However, this solution also goes along with drawbacks, as female leaders are expected to show transformational leadership behavior and thus, do not receive additional recognition when acting transformational like male leaders do (Hentschel et al., 2018). Therefore, the present study focuses on a positive leadership style that includes both communal and agentic aspects and thus, is more ambiguous regarding its fit to gender role stereotypes; precisely on authentic leadership (Monzani et al., 2021).

Authentic leadership

Authentic leadership is a positive leadership style that is grounded on other well-established positive leadership theories, such as transformational, ethical, and servant leadership (Avolio and Gardner, 2005), and that has become increasingly influential in recent years (Avolio et al., 2004; Walumbwa et al., 2008). Similarly, to how the gender equality movement started challenging the meaning of gender role stereotypes, the positive leadership movement challenged the attributes and behaviors that would describe an effective organizational leader (leader role stereotype; Monzani and Van Dick, 2020). More precisely, due to the destructive role that business leaders played after the 2008 wall street crash (Gandz et al., 2010; Crossan et al., 2017), the traditional managerial view on leadership, focusing on contingent rewards and punishments ("carrots and sticks"), lost ground to positive leader attributes and behaviors that advance the organizational goals by promoting their followers' self-actualization and well-being. Authentic leadership style itself is described by two self-based psychological mechanisms; self-awareness and self-regulation (Gardner et al., 2005), and is operationalized through four dimensions: Firstly, *self-awareness* refers to the awareness of goals, emotions, and needs of both oneself and others. Secondly, *balanced processing of information* refers to the consideration of different stakeholders' viewpoints before making important decisions. Thirdly, *relational transparency* refers to the establishment of open and clear relations with others. Lastly, *internalized moral perspective* refers to acting coherently with inner values, even in adverse contexts (Gardner et al., 2005). A myriad of studies has shown how authentic leadership predicts individual performance and loyalty above and beyond transactional leadership (Monzani et al., 2014, 2015a,b); negatively predicts employee silence (Monzani et al., 2016) and positively predicts managerial voice (Monzani et al., 2019). Further, authentic leadership predicts growth-enhancing social exchange between leaders and followers, which promotes their mutual well-being (Ilies et al., 2005; Weiss et al., 2018), and a variety of positive work outcomes, such as trust in leader and job satisfaction (see Gardner et al., 2011; Banks et al., 2016; Hoch et al., 2018).

In the realm of gender and leadership, it is important to note that authentic leadership can be seen as an androgynous leadership style (Monzani et al., 2015a,b, 2021). Authentic leadership captures agentic *and* communal leadership behaviors. Characteristics such as a higher awareness of followers' developmental needs, developing growth-enhancing relations through open and transparent communication, and by considering others' voice in decision-making are more congruent with the nurturing connotation of the female gender role (Monzani et al., 2021). Although authentic leaders can be caring and concerned for developing followers, authentic leadership also includes more agentic connotated behaviors, for instance when leaders are expected to act against strong situational or social pressures to defend their internalized values. In other words, doing "the right thing," even if unpopular, demands a high level of assertiveness and dominance, which are agentic attributes.

There is some initial evidence suggesting that authentic leadership seems to be an alternative for female leaders to overcome the hurdles created by role incongruity. More precisely, women scoring higher in authentic leadership tend to identify more with their organizations and are also less likely to make unethical business decisions (Monzani et al., 2015a,b, 2021). These two constructs, in turn, are likely to reduce female leaders' turnover intentions, and help them overcome the harsher scrutiny of their judgment calls by peers and followers that results from the double standard predicted by RCT.

Despite these encouraging findings, RCT suggests that, due to their minority status in male-dominated top management teams or executive boards, female managers may face more difficulties in achieving the relational authenticity required for being authentic leaders (Eagly, 2005). A recent study provided a complementary explanation, suggesting that the leader-gender role incongruence produces an attribution bias that affects female managers' self-reports of authentic leadership behaviors ("*the authentic-female attribution bias*"; Monzani et al., 2015a,b).

"At the workplace, based on the female gender role, women are expected to show concern for others by (1) being highly aware of their needs and values (self-awareness), (2) to be relationship-oriented and developing open relations with others, and (3) to be emphatic and to consider different viewpoints (balanced processing of information), but as managers they are expected to be more agentic and act coherently with inner values (internalized moral perspective dimension of authentic leadership) even in adverse contexts. Because of this role conflict, female managers should attribute their self-awareness, balanced processing of information, and relational transparency to their gender role and not to their leadership role, perceiving themselves less authentic as leaders." (Monzani et al., 2015a; Monzani et al., 2015b, p. 739). In other words, we propose that women do not behave less authentic as leaders than men, but because the gender role expectation for females is highly congruent with the communal aspects of authentic leadership, female managers themselves and also their followers tend to attribute these leadership behaviors to being a woman, while for male leaders, it would be attributed to being an authentic leader.

Following this line of thinking, we believe that (a) women themselves show this bias and ascribe less authentic leadership to

themselves, and (b) followers also show this bias and ascribe less authentic leadership to female leaders. Based on this logic, we formulate the following hypotheses:

> *Hypothesis 1a*: Women ascribe less authentic leadership behavior to themselves than men.
>
> *Hypothesis 1b*: Female leaders are ascribed less authentic leadership behavior by their employees compared to male leaders.

Group dynamics in leadership

Social psychologists defined leadership as "a process of social influence through which an individual enlists and mobilizes the aid of others in the attainment of a collective goal" (Chemers, 2001, p. 376). Therefore, leaders, by definition, cannot exist without followers, and often, leadership effectiveness is defined by the leaders' influence on their employees. Thus, in reality, leaders act within social groups (e.g., their teams, departments, etc.), and "leaders not only lead groups of people, but they are also themselves members of these groups" (van Knippenberg & Hogg, 2003, p. 244). Therefore, leaders' social identity, understood as "the individual's knowledge that he/she belongs to certain social groups together with some emotional and valuable significance to him/her of this group membership" (Tajfel, 1972, p. 292), plays an important role for leaders' acceptance and effectiveness (Ashforth and Mael, 1989; van Knippenberg and Hogg, 2003).

As mentioned above, a group's prototype matters to determine "who will lead and who will follow (in this group)." When defining group boundaries and characteristics, social comparison and categorization are core processes (self-categorization theory; Turner et al., 1987). For these categorization and comparison processes, individuals use prototypes as mental heuristics (Hogg, 2001). Prototypes are defined as "fuzzy sets of attributes that define and prescribe attitudes, feelings, and behaviors that characterize one group and distinguish it from other groups" (Hogg, 2001, p. 187). The Social Identity Model of Leadership (SIMOL; Hogg, 2001; van Knippenberg et al., 2004) explains how these underlying social identity and social categorization processes act in leadership emergence and effectiveness.

The SIMOL focuses on how leaders operate within social groups and the characteristics of the leader *as a group member* (van Knippenberg and Hogg, 2003). One key factor for leaders' effectiveness is their group prototypicality (van Knippenberg, 2011). When the group perceives the leader as representing the group's prototype, they will see him or her as one of them (ingroup), interpret his or her behavior positively and assume he or she is acting in favor of the ingroup (van Knippenberg and Hogg, 2003). Therefore, in organizations, followers (e.g., employees) tend to like and trust a prototypical leader more than non-prototypical leaders, they are more likely to tolerate the shortcomings of a prototypical leader and ascribe them a higher degree of leadership effectiveness (van Knippenberg and Hogg, 2003; van Knippenberg and van Knippenberg, 2005; Giessner and van Knippenberg, 2008; van Dijke and De Cremer, 2008; Giessner et al., 2009; Ullrich et al., 2009; Steffens et al., 2021). Two recent meta-analyses have confirmed the positive effects of leader group prototypicality for a range of individual and organizational constructs (Barreto and Hogg, 2017; Steffens et al., 2021). Because prototypical leaders are seen as protecting and advancing the interests of the groups they lead, we expect that team prototypicality positively relates the positive leadership styles including authentic leadership and trust in leader.

Thus, in the present study, we propose that high team prototypicality, that is when the leader resembles or embodies the group's prototype, will positively influence both the leaders' self-perceptions and their perception by followers. Leaders who perceive themselves as prototypical for the team should feel enabled to show more authentic leadership and act authentic in their leader role. Leaders who are perceived acting in the interest of the group are generally perceived as more authentic and showing authentic leadership (Steffens et al., 2016). High team prototypicality should positively relate to more (pronounced) authentic leadership and more trust in leader. This logic leads us to formulating the following hypotheses:

> *Hypothesis 2*: Leaders' team prototypicality positively relates to authentic leadership behavior, both self-reported (H2a) and as rated by the followers (H2b).
>
> *Hypothesis 3*: Leaders' team prototypicality positively relates to employees' trust in their leader.

Gender and group dynamics in leadership

Now, why should prototypicality be a key factor for female leaders to overcome role incongruity issues? Societal barriers, such as gender and leader role stereotypes, that prevent women and other equity-seeking groups from climbing a firm's hierarchical structure, are difficult to modify. Unfortunately, these stereotypes reflect the longstanding belief systems of a given society. In contrast, a group's prototype is not stable *per se*, as it depends on how the group manages the categorization processes and comparison possibilities of its members, and, thus, is inherently more fluid (Turner et al., 1987; Monzani et al., 2015a,b). Therefore, team prototypicality is a fluid property of social groups, which can be modified more easily both by organizations and leaders themselves, for example, by engaging in identity entrepreneurship behaviors (Steffens et al., 2014; van Dick et al., 2018). Combining team prototypicality and leader gender, we assume that female leaders will benefit more from high team prototypicality than male leaders. Male leaders are not confronted with biases based on role incongruity as female leaders are and experience a better fit with

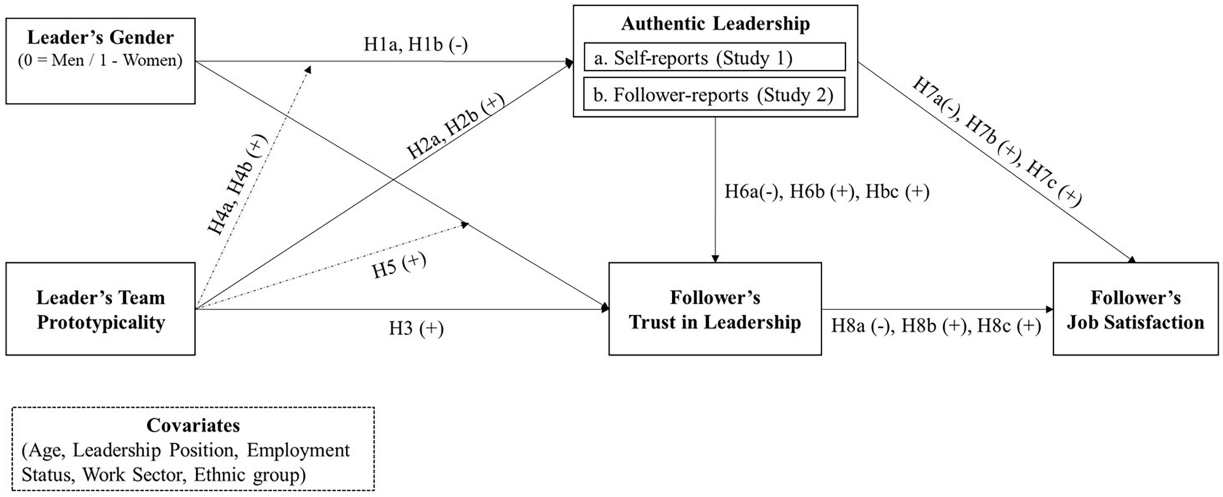

FIGURE 2
Extended theoretical model.

the leader prototype. Team prototypicality shifts the comparative dimensions from assessing a match between leader gender and leader prototype to a match between the individual leader and the team members. Therefore, female leaders who perceive themselves as representing the group they lead or who are perceived by their followers as representing the group should be evaluated based on this congruity with the team which, in turn, should reduce biased perceptions and evaluations due to the role incongruity between the female gender role and the leader role.

Thus, we argue that if the salience of a female leaders' team prototypical status is increased within the workgroup they lead, female leaders will not evaluate and not be evaluated by their followers based on societal stereotypes about gender and leader, but be perceived as representatives of the group they lead. In short, we claim that by leveraging the insights of SIMOL theory, we can expect to overcome the "double bind" that female leaders face. Therefore, we assume that the effects of high team prototypicality are stronger for female than for male leaders.

> *Hypothesis 4: Team prototypicality and leader gender interact in a way that the relation between team prototypicality and authentic leadership is stronger for female leaders both in terms of their self-perception (H4a) and employees' perception (H4b).*
>
> *Hypothesis 5: Team prototypicality and leader gender interact in a way that the relation between team prototypicality and trust in leader is stronger for female leaders.*

Follower outcomes

The right part of our extended theoretical model (see Figure 2) shows followers' job satisfaction as the main individual outcome of our extended model. While the antecedents and mechanisms predicting job satisfaction have been studied thoroughly in the past, this construct remains a worthy metric for line and talent managers alike (Judge et al., 2020). A meta-analysis by Barreto and Hogg (2017) showed that group prototypicality is a significant predictor of trust in leader. In addition, there is extant evidence on the authentic leadership literature to predict direct and indirect effects on job satisfaction and trust in leader (Gardner et al., 2011;Banks et al., 2016; Hoch et al., 2018). Further, from previous research we know that trust in leader is related to job satisfaction (Gilstrap and Collins, 2012; Braun et al., 2013; Gibson and Petrosko, 2014).

Prior studies substantiated a main effect of prototypicality on authentic leadership. For example, leaders that are perceived as championing the interest of a collective are rated as being more authentic by their followers (Steffens et al., 2016). In turn, several studies show that authentic leadership is a strong correlate of both trust in leader and job satisfaction, with meta-analytic correlations ranging between $r = 0.65$ and $r = 0.69$ for trust in leader and ranging between $r = 0.48$ and $r = 0.53$ (Banks et al., 2016; Hoch et al., 2018). Finally, early studies and reviews in the field of authentic leadership have shown that trust in leader actually mediates followers' perceptions of authentic leadership and job satisfaction (Wong and Cummings, 2009; Gardner et al., 2011; Černe et al., 2014). Building up on and combining these findings, we expect that team prototypicality has direct and indirect effects on job satisfaction as carried through authentic leadership and trust in leader, respectively.

We acknowledge that our hypotheses in this regard are rather of confirmatory, than of exploratory nature. However, we believe that replicating prior findings through hypotheses testing is important, as replication is a crucial part of the scientific process, and testing these hypotheses does not reduce the novelty of our study, which clearly lies (with) in our core model (see Figure 1)

and the interactive effect of exogenous (biological sex) and endogenous (team prototypicality) antecedents of authentic leadership. Thus, combining these findings with our core model, we predict:

> *Hypothesis 6*: Authentic leadership will mediate the indirect effect of (a) team prototypicality, (b) leader gender, and their (c) joint effect on trust in leader and job satisfaction.
>
> *Hypothesis 7*: Trust in leader will mediate the indirect effect of (a) team prototypicality, (b) leader gender, and their (c) joint effect on job satisfaction.
>
> *Hypothesis 8*: Authentic leadership and trust in leader will serially mediate the indirect effect of (a) leader gender, (b) team prototypicality, and their (c) joint effect on job satisfaction.

Adding these hypotheses to our core model (Figure 1) leads to the extended theoretical model (see Figure 2).

To test our hypotheses, we conducted two studies complementing each other. To test our core model (hypotheses H1 to H5), we first conducted an online experiment using a sample of US employees who also had leadership experience, in which we used a similar manipulation of team prototypicality as Monzani et al. (2015a,b) and asked them to report their authentic leadership behavior. Second, testing both our core and extended model, we conducted an online survey study with US employees who were asked to report their leader's gender, perceived team prototypicality and authentic leadership, their trust in leader, and their job satisfaction.

Study 1

Study 1: Methods

Participants and procedure

Study 1 consisted of an online experiment using scenarios with a single-factor between-subject design (factor: low vs. high team prototypicality). We used the online survey program Unipark of Tivian and data were collected *via* Amazon Mechanical Turk (in the following referred to as MTurk). MTurk allows recruiting and compensating participants more efficiently than other data-collection approaches. Moreover, we chose MTurk as (a) it facilitates data acquisition of participants from the population of working adults who have or have had leading responsibilities in the present or past, and (b) as MTurk offers demographic diversity and good data (Buhrmester et al., 2011; Goodman et al., 2013). Participants should be currently working and have or have had a leading position in the past. Participants were informed that the survey would examine how leaders behave in different situations and would take about 10 min on average. They received 0.75 US$ as a compensation for their participation. The study was exempt from ethics approval at Goethe University Frankfurt as it passed all major ethical criteria for research (anonymity, voluntariness, etc.). As it is recommended for researchers using MTurk to screen for participants' attention (Goodman et al., 2013), out of 430 individuals who opened/accessed the link to our study, we excluded all participants who did not provide a complete data set and/or those whose survey duration was 0. The final sample consisted of 315 (114 females, 201 males) individuals with a mean age of 33.69 years ($SD = 11.21$). Of these, 148 held a leading position (167 had no leading responsibility) and more than two-thirds of the participants (231 individuals) had a permanent contract. Two-thirds (206 individuals) worked in the private and 109 in the public sector. The majority, almost 80%, were European-American, 7.6% were African-American, 7.0% were Asian-American, 5.1% were Hispanic, and 0.3% were native Americans.

Participation in the study was voluntary and all participants provided their informed consent. At the beginning of the experiment, all participants indicated their biological sex and several other demographic variables (e.g., age, working sector, and ethnic group). After reporting their demographic information, participants were randomly assigned to one of the two experimental conditions. This manipulation of team prototypicality has already been used by Monzani et al. (2015a,b). In both experimental conditions, participants were asked to imagine to be upper managers in a multinational organization. Participants then received the results of a recent internal HR survey, which compared the fit between their scores and the scores of their team members on six key elements of their organization (vision, mission, organizational values, and culture, strategy, work processes, and career development opportunities). Thus, participants saw figures showing a high fit (65%–91%) between them and their team members on these six dimensions (high team prototypicality) or a low fit (12%–32%, low team prototypicality condition). On the following page, participants rated themselves on team prototypicality and authentic leadership. A short debriefing was provided on the screen after all scales had been completed.

Measures

Leader team prototypicality manipulation

As discussed above, we used the team prototypicality manipulation from Monzani et al. (2015a) to Monzani et al. (2015b). Depending on the experimental condition, participants read a scenario and saw figures with either high (ranging from 65% to 91%; high prototypicality condition) or low (ranging from 12% to 32%; low prototypicality condition) levels of fit to their team members.

Precisely, participants read the following:

"Now, imagine that you are high-level manager in the multinational organization EINROTH. You are leading a small team consisting of members from different areas of your organization, who are reporting directly to you. A few

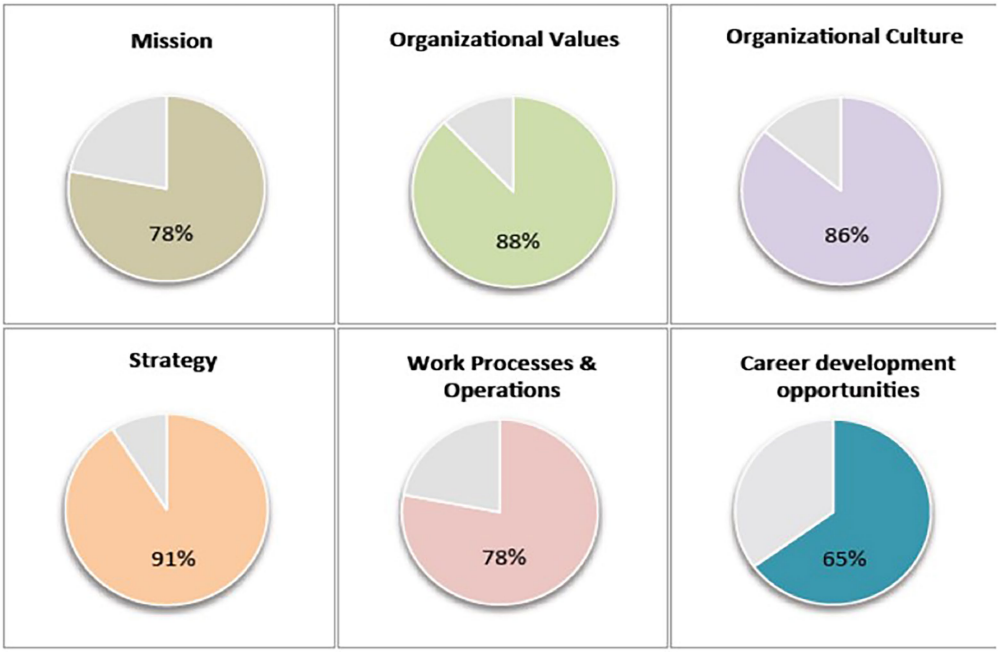

FIGURE 3
Team prototypicality manipulation (high team prototypicality condition) in Study 1.

days ago, the results of an internal survey, performed by the Human Resource Department, were sent to your work e-mail address. The survey explored how both top and middle managers understand key elements of the organization, such as its mission, its values, how effective work processes are, or if professional development opportunities are present or not. The results of this survey matched the perceptions of the team leader (you) with the views of your team. For example, the match between your average scores and your team's scores for which strategy this organization requires is 91% [24%]. Overall, these results show that you and your team have similar [different] views about the values and beliefs about this organization, its culture and how work should be done in order to be successful." Below participants saw a figure depicting their match to their team members (see Figure 3).

Team prototypicality

Team prototypicality was measured with two items (adopted from Ullrich et al., 2009; Monzani et al., 2019) on a 7-point Likert scale with values ranging from *1 = do not agree at all* to *7 = fully agree*. The two items "I represent what is characteristic for my team" and "I represent what my team has in common." showed an excellent reliability *(Cronbach's* $\alpha = 0.95$).

Authentic leadership

Authentic leadership was assessed with the Authentic Leadership Questionnaire (ALQ, Walumbwa et al., 2008). The ALQ consists of 16 items that assess the frequency of authentic behaviors in a leadership role, as captured by its four dimensions. Said behaviors were rated using a 5-point Likert scale with values ranging from *1 = not at all* to *5 = frequently*. Some exemplary items are "I say exactly what I mean" (Relational Transparency), "I make decisions based on my core values" (Internalized Moral Perspective), "I analyze relevant data before coming to a decision" (Balanced Processing of Information), and "I know when it is time to re-evaluate my position on important issues." (Self-Awareness). The ALQ yielded excellent reliability (*Cronbach's* $\alpha = 0.90$).

Gender

Gender was assessed by asking participants for their biological sex (dummy coded, 0 = male, 1 = female).[1]

Controls

Several variables were assessed as potential control variables: age in years as proxy for work experience, employment type (0 = temporary, 1 = permanent), work sector (0 = public, 1 = private), leadership responsibility (0 = no, 1 = yes), and ethnic affiliation (0 = European-American, 1 = other).

A list of all variables and constructs assessed in Study 1 including the instruction, concrete items, and answer format can be found in Table A.1 in the Supplementary material.

1 We completely acknowledge that a dichotomous measure of gender does not captures an individual's gender identity nor all biological sexes. In our recent and ongoing research, we assessed gender differently.

TABLE 1 Study 1: Results of preliminary analyses with ANCOVA.

	Authentic leadership	
	MS	*F*
Controls		
Age	0.94	3.36*
Ethnic group[a]	0.05	0.18
Leadership position[b]	1.60	5.69*
Employment status[c]	1.19	4.24*
Work sector[d]	0.03	0.09
IVs		
Team prototypicality (manipulation)	0.01	0.04
Biol. sex[e]	0.20	0.69
Gender*team prototypicality	0.03	0.09
Model R^2	0.06	

$N = 315$.
[a]0 = European-American, 1 = other.
[b]Leading position, 0 = no, 1 = yes.
[c]0 = temporary contract, 1 = permanent contract.
[d]0 = public sector, 1 = private sector.
[e]Biological sex: 0 = male, 1 = female.
*$p < 0.10$; *$p < 0.05$, two-tailed.

Data analyses

Before testing our model, we conducted an ANCOVA with gender, age, kind of contract, sector, leadership responsibility, and ethnic affiliation (0 = European-American, 1 = other) as controls. The manipulation check revealed that the manipulation worked as intended and participants in the high team prototypicality condition ($M = 5.604$) perceived themselves as more prototypical for the team than those in the low team prototypical condition ($M = 3.622$, F (1,307) = 177.232, $p < 0.001$). In addition, we conducted a preliminary analysis to test our core model using an ANCOVA with age, kind of contract, sector, leadership responsibility and ethnic affiliation as controls, participant's biological sex, and team prototypicality manipulation as between-factors. None of our factors nor their interaction term were significant (see Table 1).

Thus, we employed a more sophisticated, two-stage data analysis strategy. First, we conducted multivariate regressions to explore our predictions regarding authentic leadership, and then replicated our analyses employing a more sophisticated, covariance-based approach, that is, structural equation modeling (SEM). We believe, this dual approach provides a good trade-off between the parsimony of our model and the robustness of our findings.

To test the hypotheses on self-perception (Hypothesis 1a, Hypothesis 2a, and Hypothesis 4a), we used model 14 of the PROCESS macro version 4.0 for SPSS with 10.000 bootstrapping samples, 95% confidence intervals. Team prototypicality as a metric variable of the interaction term was mean centered. Age, ethnic affiliation (European-American vs. other), possession of a leadership position (no vs. yes), employment status (limited vs. unlimited), and work sector (private vs. public) were entered as control variables. The team prototypicality manipulation was entered as independent variable, leader's team prototypicality (scale) as mediator, biological sex as second stage moderator, and authentic leadership as dependent variable (see Table 2). In addition, we ran the model without any control variables, which did not change the pattern emerging, but slightly changed the magnitude of the results.

Therefore, in the second stage, we constructed structural equation models without controls in MPlus 8.2, following the recommendations by Kline (2013). Moreover, because simulation studies have shown that the chi-square ($\chi 2$) test is sensitive to sample size, we employed the mainstream additional goodness-of-fit indicators suggested by Cheung and Rensvold (2002). Finally, we used a robust estimator, the weighted least squares mean and variance adjuster (WLSMV) to prevent potential issues with non-normal distributions in structural equation modeling. These additional considerations allow us to ensure the robustness of our findings.

Study 1: Results

Descriptive statistics, intercorrelations, and reliabilities are displayed in Table 3. Table 3 shows that, as predicted and confirmed by our manipulation check analysis, our experimental manipulation of team prototypicality was positively and strongly correlated with participants' reports of (self-) perceived team prototypicality, suggesting that our manipulation evoked the intended effect. Further, also as expected, occupying a leadership position correlated positively with higher frequency of authentic leadership behaviors. Finally, the interaction term between participants' biological sex and our prototypicality manipulation was related to authentic leadership, justifying our subsequent regression and SEM analyses.

The full model explained 8% of variance in authentic leadership behavior. The experimental condition significantly predicted team prototypicality ($b = 1.98$, $SE = 0.15$, $t = 13.30$, $p < 0.001$). Incongruent with hypotheses 1a and 2a, neither gender ($b = 0.05$, $SE = 0.06$, $t = 0.74$, $p = 0.46$) nor team prototypicality ($b = -0.01$, $SE = 0.03$, $t = -0.25$, $p = 0.80$) significantly predicted AL. However, and in line with Hypothesis 4a, the interaction term was significant ($b = 0.09$, $SE = 0.04$, $t = 2.53$, $p = 0.01$) and associated with a significant increase in explained variance (2%). For men, there was no significant conditional effect ($b = -0.01$, $SE = 0.03$, $t = -0.25$, $p = 0.80$), whereas for women it turned out significant ($b = 0.09$, $SE = 0.03$, $t = 2.72$, $p = 0.007$; see Figure 4). This applied for the mediation similarly: The mediation was significant for women (effect = 0.17, CI95%: 0.06, 0.29), but not for men (effect = −0.01, CI95%: −0.12, 0.09). Further, the index of the moderated mediation was significant (index = 0.19, CI95%: 0.06, 0.32).[2] Figure 4 illustrates the interaction effect of team prototypicality and biological sex on authentic leadership.

2 We ran the same analysis (PROCESS model 14) in the leader subsample (n=148). The pattern of results remained the same and the interaction term team*prototypicality remained significant (p=0.038) as was the index of moderated mediation (index=0.21, CI95%: 0.04, 0.39).

TABLE 2 Study 1: Results (manifest) with control variables (PROCESS model 14; 10.000 bootstrapping samples).

	Team prototypicality (scale)					Authentic leadership			
	b		*SE*	*t*		*b*		*SE*	*t*
Constant	−1.03	**	0.30	−3.48		3.64	***	0.12	30.23
Age	−0.01		0.01	−0.69		0.01	*	0.00	1.83
Ethnic group[a]	0.10		0.19	0.51		0.01		0.08	0.18
Leadership position[b]	0.23		0.15	1.55		0.13	*	0.06	2.18
Employment status[c]	0.40	*	0.17	2.36		0.13	*	0.07	1.84
Work sector[d]	−0.38	*	0.16	−2.38		0.04		0.06	0.68
Team prototypicality manipulation	1.98	***	0.15	13.30		−0.07		0.08	−0.92
Team prototypicality (scale)						−0.01		0.03	−0.25
Biological sex[e]						0.05		0.06	0.74
Biol. Sex*prototypicality (scale)					$\Delta R^2 = 0.02$*	0.09	*	0.04	2.53
	$R^2 = 0.38$***; $f^2 = 0.61$; $1 - \beta = 0.999$					$R^2 = 0.08$***; $f^2 = 0.09$; $1 - \beta = 0.951$			

$N = 315$. f^2 = Cohen's f^2; $1 - \beta$ = Achieved statistical power.
[a]Leadership position, 0 = no, 1 = yes.
[b]0 = temporary contract, 1 = permanent contract.
[c]0 = public sector, 1 = private sector.
[d]0 = European-American, 1 = other.
[e]0 = male, 1 = female.
*$p < 0.10$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$, all two-tailed.

TABLE 3 Study 1: Means, standard deviations, intercorrelations, and reliabilities.

	M	*SD*	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	
1. Age	33.690	11.21	–[f]								
2. Ethnic group[a]	0.20	0.40	−0.142*	–[f]							
3. Leading position[b]	0.47	0.50	0.095*	−0.001	–[f]						
4. Employment status[c]	0.73	0.44	0.109*	0.019	0.107*	–[f]					
5. Work sector[d]	0.65	0.48	0.097*	−0.047	0.096*	0.014	–[f]				
6. Leader's biol. sex[e]	0.36	0.48	0.123*	−0.003	−0.007	0.081	−0.091	–[f]			
7. Leader team prototypicality manipulation	0.51	0.50	−0.073	−0.008	−0.002	−0.048	−0.008	−0.025	–[f]		
8. Perceived prototypicality (scale)	4.63	1.66	−0.071	0.030	0.067	0.081	−0.109*	0.047	0.595***	(0.95/[f])	
9. Authentic leadership	3.98	0.54	0.135*	0.012	0.159**	0.147**	0.037	0.067	−0.031	0.059	(0.90/0.90)

$N = 315$. Internal consistency estimates (Cronbach's α/McDonalds ω) are displayed on the diagonal in parentheses.
[a]0 = European-American, 1 = other.
[b]Leading position, 0 = no, 1 = yes.
[c]0 = temporary contract, 1 = permanent contract.
[d]0 = public sector, 1 = private sector.
[e]Biological sex: 0 = male, 1 = female.
[f]Not applicable.
+$p < 0.10$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$, all two-tailed.

Structural equation modeling

The results of our structural equation modeling align with our multivariate regression analyses. Both the measurement model [$\chi 2(205) = 487.40$, $\chi 2/df = 2.38$; RSMEA = 0.07, CFI = 0.95, TLI = 0.94, SRMR = 0.10] and the SEM [$\chi 2(192) = 423.66$, $\chi 2/df = 2.22$; RSMEA = 0.06, CFI = 0.95, TLI = 0.94, SRMR = 0.10] showed excellent fit to our data. The SEM model explained slightly less variance than our regression model ($R^2 = 0.07$). As expected, the measurement model shows that our independent variables were uncorrelated, and all items of authentic leadership significantly loaded onto their respective dimensions with acceptable values. Only one item showed a loading lower than 0.50 (Item 5). In turn, each dimension showed significant loadings onto the higher-order construct (authentic leadership) with significant second-order loadings ranging from 0.89 to 0.95. The result pattern remained and further corroborated the results of the manifest analyses. Figure 5 illustrates the retained SEM model.

Additional manipulation checks

Our SEM model allowed us to conduct a more robust check regarding our experimental manipulation of (leader) team prototypicality. More precisely, occupying a leadership position

might have elicited perceptions of team prototypicality in our participants. If that was the case, we would expect a main effect of leadership position on team prototypicality perceptions, or even an interactive effect with participants' biological sex. In contrast, we did not detect any main or interactive effects of leadership position on perceptions of team prototypicality. Further, we tested if biological sex would moderate the effect of occupying a leadership position on perceptions of authentic leadership. Interestingly, after controlling for manipulated and perceived team prototypicality, this effect turned out non-significant. Although at first sight, this finding might seem trivial, it further demonstrates that the double bind and prejudice that women face in leadership roles is not a mere structural or quotas issue (occupying a position or not, regardless of gender), but also an issue of psycho-social nature (women, regardless of their leadership position, tend to report both lower team prototypicality and authentic leadership).

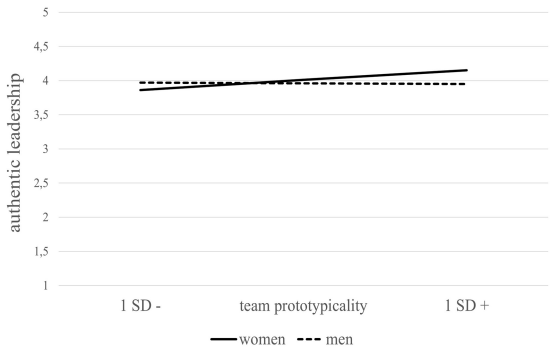

FIGURE 4
Study 1—Interactive effects between participants' biological sex and team prototypicality manipulation (high vs. low) on authentic leadership.

Study 1: Discussion

Neither the preliminary analysis nor the more sophisticated analyses in Study 1 supported hypotheses 1a and 2a. There were gender differences in self-reported authentic leadership, nor did leaders' team prototypicality influence AL. Although not visible in the preliminary analysis (very likely due to restricted variance of the dichotomous nature of the experimental condition team prototypicality factor), Study 1 provided initial support for our theorizing, in that high team prototypicality helps women feel more authentic when occupying a leader role. More precisely, when women perceived themselves as being prototypical for their teams—as induced by the experimental condition and confirmed by the manipulation check—they reported significantly higher AL. Additionally, our confidence in our findings is strengthened by the fact that we found this result/pattern both in manifest and latent analyses testing our hypotheses.

This study has some strengths and some obvious limitations. In terms of strengths, we employed exogenous variables as predictors, and randomly assigned participants to our experimental conditions.

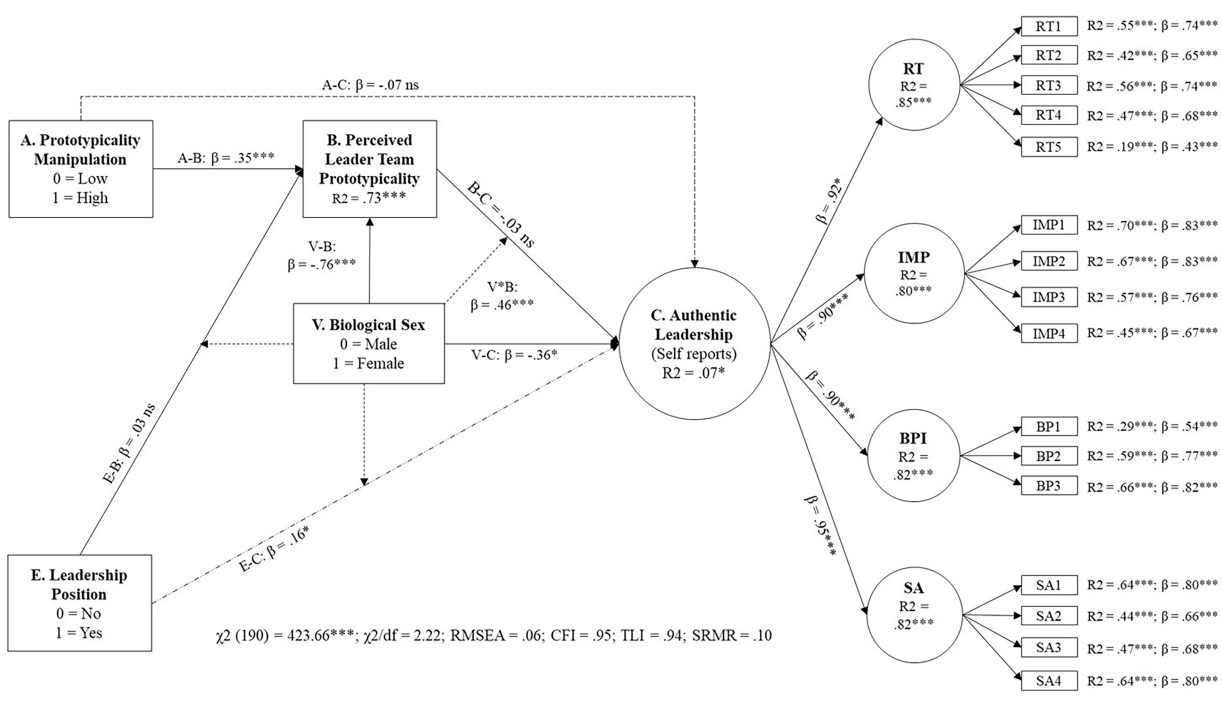

FIGURE 5
Study 1—Results of a SEM testing Hypotheses 1a, 2a, and H4a (self-perception perspective).

Due to these strengths in design, we do not anticipate concerns about potential endogeneity issues when making our causal claims (Antonakis et al., 2010). Similarly, because we used a manipulation, biological gender, and self-reports, at first glance, we do not have any concerns regarding common method variance (Podsakoff et al., 2012). Taken as a whole, these precautions increase our confidence in the robustness of our results. However, one limitation of Study 1 is that we only assessed and tested the effect of team prototypicality on self-perceived and self-reported authentic leadership, using a scenario-based online experiment. Therefore, participants' answers might be influenced by ego-protective biases. Yet, self-perception only tells half of the story. Thus, to strengthen our argument and complement the findings of Study 1, we conducted an online survey, in which we assessed followers' perceptions of their leader as well as their own attitudes.

Study 2

In Study 1, we showed that women's self-ratings in AL were positively affected by team prototypicality. Being assigned to the high team prototypicality condition lead to higher authentic leadership especially in female participants. Extending these results, in Study 2, we examined the effects of leaders' team prototypicality and leader gender on other-reported authentic leadership behavior and employees' trust in leader (Podsakoff et al., 1990; Burke et al., 2007).

Study 2: Methods

Participants and procedure

Participants were US employees who participated in an online questionnaire that was programmed in the software Unipark by Trivian and the survey was then posted on Amazon's Mechanical Turk platform addressed at currently working people. Despite its critics, some studies show that the practical benefits of these platforms (higher sampling heterogeneity and diversity, real working population vs. students), outweigh its limitations (Buhrmester et al., 2011). A total of 346 individuals participated in the survey. We deleted participants with missing data, the test trial participations from the research team members, and those with suspicious answer patterns (like always the same number—even in reversed items). Thus, our final sample consisted of 300 participants (111 female) with a mean age of 31.71 years ($SD = 9.53$). Eighty-eight participants had a leadership position themselves and 212 had no leading position. The majority (222 individuals) had a permanent contract and only 78 participants had a temporary contract. Almost 60% (176 participants) worked in the private sector, and 124 participants worked in the public sector. The majority (76.3%) were European-American, 10.3% were African-American, 9.0% were Asian-American, 4.0% were Hispanic, and 0.4% were native Americans.

At the beginning of the survey, participants indicated some demographical variables like participants' biological sex, age, and their leaders' biological sex. Then, they rated their leader's authentic leadership behavior and team prototypicality. Afterward, employees rated themselves on some employee variables like trust in leader. Again, participation in the study was voluntary and all participants provided their informed consent. Participants received a US-$1 show-up fee for taking part of our study.

Study 2: Measures

Authentic leadership

As in Study 1, authentic leadership was assessed with the 16 items of the Authentic Leadership Questionnaire (ALQ, Walumbwa et al., 2008) on a 5-point Likert scale with values ranging from *1 = not at all* to *5 = frequently*. Because employees should rate their leader, we used the other-reports version instead of self-report version. Again, the ALQ had excellent reliability in this second dataset (*Cronbach's* $\alpha = 0.94$).

Team prototypicality

Four items (adopted from Ullrich et al., 2009) assessed the leaders' team prototypicality rating. The four items were "He or she represents what is characteristic for my team.," "He or she is a good example of the kind of people that are in my team.," "He or she stands for what people who work in my team have in common.," and "He or she is very similar to most people in my team.." Participants rated on a 5-point Likert scale with values ranging from *1 = strongly disagree* to *5 = fully agree* how much the items applied to their leader. The scale showed an excellent reliability *(Cronbach's* $\alpha = 0.93$).

Job satisfaction

Based on Spector (1985), we used five items to assess job satisfaction. Thereby, we asked participants how satisfied they are with (a) their salary, (b) their leader, (c) their colleagues, (d) the work itself, and I overall. Participants rated on a 5-point Likert scale their degree of satisfaction (*1 = very dissatisfied* to *5 = very satisfied)*. The mean of these items was used as a measure of overall job satisfaction. The scale showed good reliability (*Cronbach's* $\alpha = 0.80$).

Trust in leader

Trust in leader was assessed with three items (Podsakoff et al., 1990). The items were "I feel quite confident that my supervisor/leader will always treat me fairly," "My supervisor/leader would never try to gain advantage by deceiving workers," and "I have complete faith in the integrity of my supervisor/leader." Participants indicated how much these items applied to their leader (*1 = strongly disagree* to *5 = fully agree*). The items showed excellent reliability (*Cronbach's* $\alpha = 0.93$).

TABLE 4 Study 2: Means, standard deviations, intercorrelations, and reliabilities.

	M	*SD*	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
1. Age	31.71	9.53	–[f]										
2. Ethnic group[a]	0.24	0.43	−0.150**	–[f]									
3. Leadership position[b]	0.29	0.46	0.094	−0.083	–[f]								
4. Employment status[c]	0.74	0.44	0.098*	−0.117*	0.098*	–[f]							
5. Work sector[d]	0.59	0.49	0.116*	0.085	−0.009	−0.004	–[f]						
6. Participant's biol. Sex[e]	0.37	0.48	0.170**	−0.053	−0.008	0.029	−0.142*	–[f]					
7. Leader's biol. Sex[e]	0.40	0.49	0.110*	0.010	0.012	−0.059	−0.006	0.361***	–[f]				
8. Team prototypicality	3.81	0.94	0.093	0.010	−0.032	0.079	−0.017	0.051	−0.001	(0.93)			
9. Authentic leadership	3.69	0.76	0.033	0.028	−0.024	0.094	−0.064	0.109*	−0.039	0.737***	(0.94)		
10. Job satisfaction	3.59	0.79	0.136*	−0.077	0.084	0.091	−0.088	0.094	−0.081	0.541***	0.573***	(0.80)	
11. Trust in leader	3.84	1.10	−0.031	0.028	0.044**	0.116*	−0.074	0.089	−0.075	0.694***	0.781***	0.620***	(0.93)

$N = 300$. Internal consistency estimates (Cronbach's α) are displayed on the diagonal in parentheses.
[a]0 = European-American, 1 = other.
[b]0 = no, 1 = yes.
[c]0 = temporary contract, 1 = permanent contract.
[d]0 = public sector, 1 = private sector.
[e]0 = male, 1 = female.
[f]Not applicable.
*$p < 0.10$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$, all two-tailed.

Leader's gender

Leader's gender was assessed by asking participants for the biological sex of their leader (dummy coded, 0 = "male, 1 = "female").

Controls

Participant's gender was assessed by asking participants for their anatomical sex (dummy coded, 0 = male, 1 = female). Further, age in years as a proxy for work experience was included as control. Additional dummy coded controls were employment status (0 = temporary, 1 = permanent), work sector (0 = public, 1 = private), leadership responsibility (0 = no, 1 = yes), and ethnic affiliation (0 = European-American, 1 = other).

A list of all variables and constructs assessed in Study 2 including the instruction, concrete items and answer format can be found in Table A.2 in the Supplementary material.

Study 2: Results

Descriptive statistics, intercorrelations and reliabilities are displayed in Table 4. For testing our core hypotheses H1 to H5, we used model 1 of PROCESS version 4.0 with 10,000 bootstrapping samples. Team prototypicality as metric variable of the interaction term was mean centered. Age, ethnic affiliation (European-American vs. other), possession of a leadership position (no vs. yes), employment status (limited vs. unlimited), and work sector (private vs. public) were entered as controls in all analyses.[3] Authentic leadership was entered as dependent variable for testing hypotheses H1b, H2b, and H4b. Trust in leader was entered as dependent variable for testing hypotheses H3 and H5.

Manifest testing of core model

Authentic leadership

The full model explained 56% of variance in authentic leadership (AL). Leader's gender ($b = -0.05$, $SE = 0.06$, $t = -0.81$, $p = 0.42$) was not significant and hypothesis 1b was not supported. However, team prototypicality ($b = 0.51$, $SE = 0.04$, $t = 12.07$, $p < 0.000$) and its interaction with leader gender ($b = 0.19$, $SE = 0.06$, $t = 2.98$, $p = 0.003$) was significant. The interaction term was associated with a significant increase in explained variance (1.3%, $p = 0.003$, see Table 5). Subsequently conducted simple slope analyses showed that both slopes were significant; however, the slope for women was slightly steeper ($b = 0.70$, $SE = 0.05$, $t = 14.81$, $p < 0.001$) than the slope for men ($b = 0.50$, $SE = 0.04$, $t = 12.07$, $p < 0.001$; see Figure 6). Thus, hypothesis 2b was supported.

Trust in leader

The full model explained 51% of variance of trust in leader. Supporting hypothesis 3, team prototypicality ($b = 0.73$, $SE = 0.06$, $t = 11.26$, $p < 0.000$) was a significant predictor of trust in leader. Leader gender ($b = -0.14$, $SE = 0.09$, $t = -1.47$, $p = 0.14$) was not significant, but the interaction of team prototypicality and leader gender ($b = 0.20$, $SE = 0.10$, $t = 2.07$, $p = 0.040$) was significant. The interaction term was associated with a significant increase in explained variance (0.7%, $p = 0.040$, see Table 5). Subsequently, the simple slope analysis conducted showed that both slopes were significant, however, the slope for female leaders was slightly steeper ($b = 0.93$, $SE = 0.07$, $t = 12.87$, $p < 0.001$) than the slope for

3 We also ran the analyses without control variables. Thereby, the pattern of results remained the same and only differed in its magnitude.

TABLE 5 Study 2: Results of hierarchical regression predicting authentic leadership and trust in leader (core model).

		Authentic leadership					Trust in leader			
		b		*SE*	*t*		*B*		*SE*	*t*
Constant		3.87	***	0.14	27.12		4.26	***	0.22	19.57
Participants' age		−0.00		0.00	−0.96		−0.01	*	0.01	−2.37
Ethnic group[a]		0.04		0.07	0.60		0.06		0.11	0.56
Leadership position[b]		0.01		0.07	0.10		0.18	*	0.10	1.78
Employment status[c]		0.07		0.07	1.01		0.15		0.10	1.48
Work sector[d]		−0.07		0.06	−1.23		−0.11		0.09	−1.23
Team prototypicality		0.51	***	0.04	12.07		0.73	***	0.06	11.26
Leader's biol. Sex[e]		−0.05		0.06	−0.81		−0.14		0.09	−1.47
Leader's biol. Sex*team prototypicality	$\Delta R^2 = 0.01$**	0.19	**	0.06	2.98	$\Delta R^2 = 0.01$*	0.20	*	0.10	2.07
		$R^2 = 56$***; $f^2 = 1.27$; $1 - \beta = 0.999$					$R^2 = 51$***; $f^2 = 1.04$; $1 - \beta = 0.999$			

$N = 300$. f^2 = Cohen's f^2; $1 - \beta$ = Achieved statistical power.
[a]0 = European-American, 1 = other.
[b]0 = no, 1 = yes.
[c]0 = temporary contract, 1 = permanent contract.
[d]0 = public sector, 1 = private sector.
[e]0 = male, 1 = female.
*$p < 0.10$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$, all two-tailed.

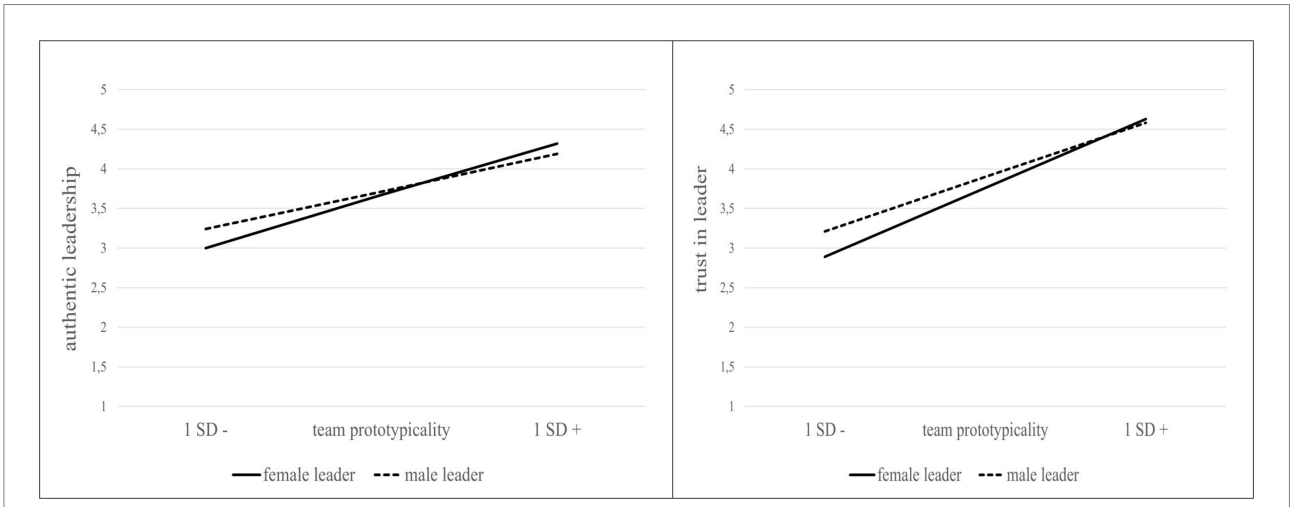

FIGURE 6
Study 2—Interaction between leader gender*team prototypicality predicting authentic leadership (left) and trust in leader (right).

male leaders ($b = 0.73$, $SE = 0.06$, $t = 11.26$, $p < 0.001$; see Figure 6). Thus, hypothesis 5 was supported.

Testing the extended model with structural equation modeling

Both our measurement model [($\chi 2$ (323) = 683.30, $\chi 2$/df = 2.12; RSMEA = 0.06, CFI = 0.97, TLI = 0.97, SRMR = 0.05)] and SEM models [($\chi 2$ (205) = 487.40, $\chi 2$/df = 2.38; RSMEA = 0.07, CFI = 0.95, TLI = 0.94, SRMR = 0.10)] showed a good fit to our data. Figure 7 shows the standardized loadings and regression coefficients. Overall, the SEM model shows a similar pattern of results as those detected in our multivariate regression (except for hypothesis 1b). Further, we used the "INDIRECT" command in Mplus for obtaining standardized indirect effects in order to test our hypotheses H6a–H6c, H7a–H7c, and H8a–H8c.

Authentic leadership mediated the indirect effect of leader's gender on trust in leader [β = −0.38 (0.11), $p < 0.001$]. Similarly, authentic leadership mediated the specific indirect effect of team prototypicality on trust in leader [β = 0.46 (0.04), $p < 0.0001$] and their joint effect [β = 0.38 (0.12), $p < 0.002$]. Similarly, authentic leadership mediated the specific indirect effect of leader gender on job satisfaction [β = −0.11 (0.05), $p < 0.05$] and the indirect specific effect of team prototypicality on job satisfaction [β = 0.13 (0.06), $p < 0.03$]. Similarly, the indirect specific joint effect of leader

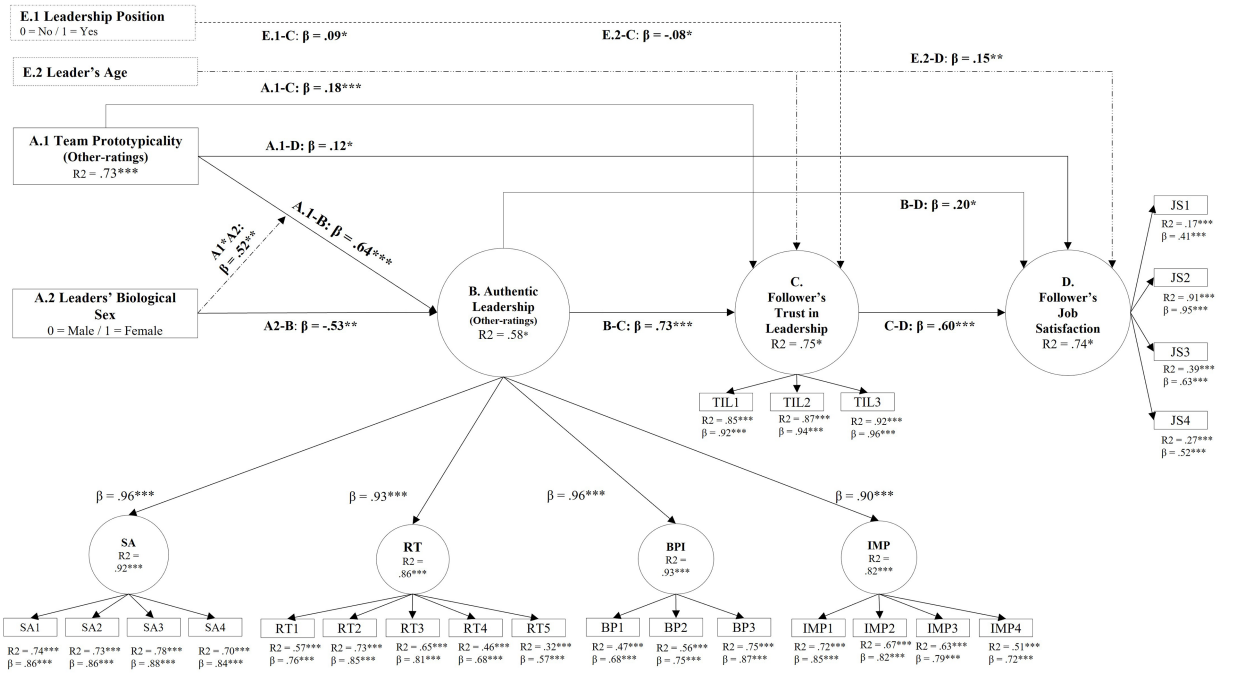

FIGURE 7
Study 2—SEM model illustrating direct and indirect effects of leader's biological sex and team prototypicality on follower's trust in leader and job satisfaction.

gender and team prototypicality as mediated by authentic leadership was also significant [β = 0.11 (0.06), $p < 0.05$]. These results provide support to hypotheses H6a, H6b, and partially support H6c.

In contrast, trust in leadership did not mediate the effect of leader gender on job satisfaction [β = 0.01 (0.10), $p < 0.95$]. Similarly, trust in leader did not mediate the joint effect of leader's gender and team prototypicality on job satisfaction [β = −0.02 (0.11), $p < 0.86$]. Yet, trust in leadership mediated the specific effect of team prototypicality on job satisfaction [β = 0.11 (0.03), $p < 0.001$]. These results only provide support for hypotheses H7b, but not H7a nor H7c.

Finally, we explored the serial mediation effects of authentic leadership (first stage mediator) and trust in leader (second stage mediator) on job satisfaction. Again, both authentic leadership and trust in leadership significantly mediated the indirect effect of leader gender [β = −0.23 (0.08), $p < 0.003$] and of team prototypicality [β = 0.28 (0.04), $p < 0.0001$]. Finally, these two constructs mediated the joint effect of leader gender and team prototypicality on job satisfaction [β = 0.23 (0.08), $p < 0.006$]. Taken together, these results provide support for hypotheses H8a, H8b, and H8c.

Study 2: Discussion

The SEM analyses supported Hypothesis 1b as there were substantive gender differences in authentic leadership in the extended model. However, H1b was not supported in testing the core model H1b. Hypothesis 2b was supported in testing of both the core model and the extended model, as team prototypicality was positively related to follower-reported authentic leadership. In addition, this relation was moderated by leader gender and was stronger for female leaders than for male leaders, as found in both the testing of the core and the extended model. Thus, hypothesis 4b was supported. Leaders' team prototypicality helped female leaders to be perceived as authentic leaders by their employees. Further, the regression analyses testing our core model showed that team prototypicality positively related to trust in leader (supporting Hypothesis 3) and this effect was moderated by leader gender and, as expected, was stronger for female leaders (supporting hypothesis 5).

In addition, the results of our SEM model show that the interactive effect of leader gender and perceived team prototypicality on trust in leader, was mediated by authentic leadership[4]. Thus, our mediation hypotheses for authentic

4 We verified this finding using two analytical techniques: When authentic leadership was entered as predictor in the regression model, the interaction term no longer was a significant predictor. This pattern also applied when employing a covariance approach (SEM model): the interaction (joint effect) term only predicted trust in leader and job satisfaction when mediated by authentic leadership (and then trust in leader). For parsimony reasons, we only report the latter in the paper.

leadership were supported (H6a, H6b) or partially supported (H6c). This result aligns with the findings of Steffens et al. (2016), which suggest that for leaders to be deemed authentic, at first, they need to embody the prototype of the group they lead, but also be seen as advancing and protecting its interests.

Our study also shows that team prototypicality increases the authenticity of female leaders in their followers' eyes, which, in turn, increases their trust and, eventually, their job satisfaction. This fact is evidenced in the single slopes of our multivariate regression and the positive sign of the joint indirect effect on trust in leader and job satisfaction (supporting hypotheses 8a, 8b, and 8c).

The fact that trust in leader alone did not mediate the effect of leader gender on job satisfaction is an intriguing finding of our study. It evidences the double-bind and prejudice that female leaders face, as suggested by RCT. By isolating specific indirect effects on a SEM mode, we can evince how female leaders are trusted less by their followers and how the latter report lower levels of job satisfaction, as well. Luckily, our second study also illustrates the value of both team prototypicality and authentic leadership for transcending these unfortunate biases.

General discussion

The main goal of the present study was to explore if team prototypicality (i.e., being representative of the team one is leading) can reduce prejudice and double standards that women face when occupying a leadership role. We grounded our predictions in Role Congruity Theory (Eagly and Karau, 2002) and the Social Identity Model of Leadership (Hogg, 2001). Based on prior findings, our core claim was that high team prototypicality—although generally associated with positive effects for leaders—might be a key for women and female leaders to overcome role incongruity issues. We argue that team prototypicality shifts the evaluation frame from higher-order categories like gender and leader roles away to more concrete, group-related aspects and thereby reduces biases that stem from the incongruity between the female gender role and the leader role. This process should affect both self-perceptions and perceptions by followers. Female leaders who perceive themselves as representative of the team and those who are perceived as representative of the team by their followers should score higher on authentic leadership and be trusted more. Indeed, we found support for this rationale in both studies.

We chose authentic leadership due to its combination of communal and agentic connotated behaviors to examine the potential of team prototypicality for female leaders. Despite its androgynous character, we assumed to find the general think manager-think male pattern reflected in higher scores in authentic leadership for male compared to female leaders (Hypothesis 1). However, regarding Hypothesis 1, we found mixed results. H1 was not supported in self-perception but could be supported for follower-perception in the SEM testing of the extended model. A potential reason might lie in the androgynous nature of authentic leadership and the ongoing development of leadership roles becoming less masculine, as evidenced in more recent studies, i.e., by Koenig et al. (2011). This might reduce gender and leader role driven differences between female and male leaders.

In line with the SIMOL and previous research (Giessner and van Knippenberg, 2008; Giessner et al., 2009; Ullrich et al., 2009; van Knippenberg, 2011), in Study 2, team prototypicality positively related to authentic leadership (H2b) and trust in leader (H3). Yet there was no relation between prototypicality and the self-ascription of authentic leadership in Study 1 (H2a). One possible explanation could be that the scenario induced team prototypicality (low vs. high) evokes a weaker impact than actually experienced team prototypicality in reality.

Our results supported Hypotheses 4 and 5, which predicted that the positive relations of team prototypicality and authentic leadership as well as trust in leader are stronger for female than for male leaders. The relation between team prototypicality and authentic leadership was stronger for women (H4) and they benefitted more from high team prototypicality. This pattern was stable among both self-perceptions (Study 1) and follower ratings (Study 2). Further, a similar pattern was found for the relation between team prototypicality and trust in leader (H5; Study 2). Female leaders profit more, compared to male leaders, when their followers perceive them as highly prototypical for the team.

Finally, our SEM model provided full or partial support for the indirect joint effect of leader gender and team prototypicality in two important follower outcomes, trust in leader and job satisfaction. This is not a trivial finding, as indirect effects capture the otherwise hidden synergies among constructs. In our second study, we found moderate to large indirect effect sizes, which is not common in the literature when testing (serial) mediation models.

In summary, these results highlight the relevance of considering individual and contextual factors in female leadership research (i.e., being authentic and prototypical). For example, Gloor et al. (2020) showed that teams' gender diversity influences the evaluation of female and male leaders in a way that if there is a higher proportion of women, female leaders are perceived as more prototypical. Our research even goes beyond this pure gender-based definition and perception of general prototypicality and shows that team prototypicality—which is more proximal and amenable by both the leader and the organization—seems to be one crucial factor for women overcoming obstacles based on role incongruity and a promising venue for future research and interventions.

Theoretical implications

Our work provides a theoretical contribution to gender inequality by combining RCT and SIMOL theories.

We provide initial evidence on how the in-group phenomenon, such as team prototypicality, can reduce the negative effects of traditional, societal gender role stereotypes on the advancement of women into leadership positions. In line with the point of Eagly (2005), if we are to reduce the prejudice and discrimination that women suffer, we need to find new ways to challenge a group's prototype of what an "effective leader" looks like, so that it is no longer based on traditional role stereotypes. Thus, focusing on team prototypicality and the (perceived) match of the leader to its followers—not based on gender, but on more dimensions—reduces the biases based on gender and leader role incongruity. Whereas organizational or industry-related prototypicality per definition are focusing on being representative for more distal, higher-order categories, team prototypicality shifts the focus to more proximal, team-, value-and work-related categories. We believe that this shift also leads to a change in the evaluation frame that both individuals use to evaluate themselves as team leaders and that is used by others to evaluate their team leaders. Thereby, mismatched perceptions of female leaders that stem from the incongruity between higher-order categories of the male connotated leader and the female gender role stereotype should be reduced. Further, we believe that such a shift toward the group and team as evaluative frame might be a chance not only for female leaders, but also for minority members who face discrimination and biases due to the use of higher-order social categories like ethnic background. Therefore, we encourage future research to examine the potential of team prototypicality to reduce social category-based biases in the realm of leadership beyond gender.

In this paper, we combined two conceptions of leadership: a leader-oriented approach (authentic leadership) and a group-oriented approach (SIMOL). We chose authentic leadership due to its androgynous conception and inclusion of both communal and agentic behaviors and its well-established positive outcomes (Gardner et al., 2011; Banks et al., 2016; Hoch et al., 2018). We chose the SIMOL due to its focus on group dynamics and its positive outcomes (Barreto and Hogg, 2017; Steffens et al., 2021). As outlined in the previous paragraph, we believe that when focusing on the team level, team prototypicality might shift the comparative dimension that is used for the evaluation of leaders and, thereby, allows to reduce biases based on the incongruity between the leader and female gender role. As assumed and shown, neither approach on its own is sufficient to break the double bind that women suffer in leadership positions. However, following the theoretical rationale provided by Eagly (2005), the present study shows that when these two complementary perspectives are considered together, their joint effect contributes to overcoming the barriers that role stereotypes create for female leaders. So, if women perceive themselves but also are perceived as prototypical of the team they are leading, they will likely show a higher frequency of authentic leadership and are trusted more by their followers. Thus, the general positive consequences of team prototypicality are reinforced for female prototypical leaders as they benefit from the shift of the comparative frame more than men do. In this regard, we heed Avolio's (2007) call to promote more integrative strategies in the leadership research and practice.

From the above, it follows that embracing a more holistic view of leadership is a promising avenue for future research, especially when examining gender equality in leadership. The Social Identity Model of Leadership has been recently expanded into the Identity Leadership framework by Haslam et al. (2021). The identity leadership framework suggests that in addition to prototypicality, leaders can be effective by shaping their group's sense of a common identity by three paths, namely advancement, entrepreneurship, and impresarioship. Steffens et al. (2014) developed the identity leadership inventory to measure these aspects of identity leadership and recently van Dick et al. (2018, 2021) validated the inventory in a global study across 30 different countries on all continents. As the other dimensions of the ILI also focus on the leader as team member and acting in the group's interest, future research should examine if other dimensions of identity leadership can also be converted into an advantage for female leaders—either alone or in combination with prototypicality. Further studies might attempt to replicate our findings in larger cross-cultural samples, to avoid the pitfall of generalizing insights of Western cultures into other cultures that might differ in their values, and thus also differ in their traditional role stereotypes (Obioma et al., 2021).

Practical implications

Our research shows the potential of team prototypicality as a facilitator for female leaders. One advantage of team prototypicality is that it is not a stable construct, but it is malleable and influenced by group dynamics. Thus, team prototypicality perceptions can be increased by leaders themselves by actively being entrepreneurs of their identity (Reicher et al., 2005), e.g., *via* increasing their perceived team prototypicality by approval-seeking out-group behaviors or by reconstructing the social context by creating intergroup competition (van Knippenberg and Hogg, 2003). Although we think that this approach can be a promising one for female leaders to reduce biases based on role incongruity, in our view the burden should not lie in the hand of female leaders. Moreover, organizations and upper management could support the team prototypicality perceptions of female leaders by subtle highlighting the fit of the (female) leaders and the work group they are leading.

Further, if an in-group phenomenon, such as team prototypicality, can reduce the effects of traditional societal role stereotypes, then something similar might occur within an organization's culture. Consequently, organizations can take action to shape a positive and inclusive culture, even in

societies with strong traditional role stereotypes. When organizational culture acknowledges and values both masculine and feminine connoted attributes in their leaders, such a positive organizational culture would reduce general biases based on role congruity for female leaders—in both their self-perception and the perception by their employees and coworkers—independent of the team prototypicality.

Finally, our findings also have implications for project managers and team leaders who operate in firms whose cultures promote toxic masculinity (e.g., investment banking, military, etc.). Again, if in-group dynamics can over-ride the negative effect of a toxic organizational culture in their employees, then project managers and team leaders have the possibility to take action by (re)shaping the prototype of the workgroup and values of the workgroup so that it becomes more inclusive with regards to women (and other minorities) occupying a leadership role.

Strengths and limitations

Our research is a first step, but of course, future research could build on these results and overcome some limitations. First, future studies should examine the effect of different manipulations of team prototypicality, as in the present study manipulation was solely based on work-related characteristics. Future research should examine the effects of team prototypicality by using manipulations that include personal values, personality, or a combination of different aspects. Second, we exclusively focused on prototypicality at the team level. Although we believe that team prototypicality is the most promising focus of prototypicality to override or reduce biases and discrimination based on the more abstract categories of gender and leader roles, future research should also examine the properties of other foci of prototypicality (e.g., organizational prototypicality). Third, we used cross-sectional survey data in Study 2. This design *per se* does not allow to draw causal conclusions and might be prone to common method bias. Yet, as we find similar patterns in both the experimental (Study 1) and the cross-sectional (Study 2) design, used different indicators (e.g., manipulation, self-reports) and the biological sex of the leader as key variables in both studies, which should not be influenced by common method bias (Podsakoff et al., 2003, 2012), in our opinion, the risk of false conclusions based common-method bias is very small. However, future research should replicate our findings by using multi-level data to compare the effects of leaders' self-perceived prototypicality and leaders' prototypicality perceived by the employees of female compared to male leaders. Further, using longitudinal data would allow tracking the evolvement of team prototypicality perceptions – contingent of certain leader behaviors – and its effects over time. Despite the limitations, the fact that we replicated our findings across two studies involving different perspectives, makes us confident in our results.

Conclusion

Statistics show that even after 20 years of academic insight on how to reduce gender inequality in leadership, there is still a long way to go. The present study provides evidence on how ingroup dynamics in form of team prototypicality can support leaders, especially female leaders, to unleash their true leadership potential.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. The patients/participants provided their written informed consent to participate in this study.

Author contributions

AH, LM, and RD contributed to the development and design of the research. AH organized data collection, performed the initial statistical analyses and all manifest analyses, wrote the first draft of the manuscript and its revisions. LM performed the latent analyses. Both LM and RD revised the first draft of the manuscript critically and checked the revised versions. All authors contributed to the article and approved the submitted version.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2022.859577/full#supplementary-material

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Heavier Lies Her Crown: Gendered Patterns of Leader Emotional Labor and Their Downstream Effects

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Women use power in more prosocial ways than men and they also engage in more emotional labor (i.e., self-regulate their emotions to respond and attend to the needs and emotions of other people in a way that advances organizational goals). However, these two constructs have not been previously connected. We propose that gendered emotional labor practices and pressures result in gender differences in the prosocial use of power. We integrate the literature on emotional labor with research on the psychology of power to articulate three routes through which this happens. First, women may be more adept than men at the intrapersonal and interpersonal processes entailed in emotional labor practices—a skill that they can apply at all hierarchical levels. Second, given women's stronger internal motivation to perform emotional labor, they construe power in a more interdependent manner than men, which promotes a more prosocial use of power. As a result, female powerholders tend to behave in more prosocial ways. Third, when they have power, women encounter stronger external motivation to engage in emotional labor, which effectively constrains powerful women's behaviors in a way that fosters a more prosocial use of power. We discuss how, by promoting prosocial behavior among powerholders, emotional labor can be beneficial for subordinates and organizations (e.g., increase employee well-being and organizational trust), while simultaneously creating costs for individual powerholders, which may reduce women's likelihood of actually attaining and retaining power by (a) making high-power roles less appealing, (b) guiding women toward less prestigious and (c) more precarious leadership roles, (d) draining powerful women's time and resources without equitable rewards, and (e) making it difficult for women to legitimize their power in the eyes of subordinates (especially men). Thus, emotional labor practices can help explain the underrepresentation of women in top leadership positions.

Keywords: emotional labor, gender, power, leadership, emotion, prosocial behavior

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INTRODUCTION

When they have power, women tend to behave in more prosocial ways than men. For example, a meta-analysis of 162 studies by Eagly and Johnson (1990) found a stronger tendency in women than in men to lead in an interpersonally oriented style in laboratory experiments. Across studies, women in positions of authority were more likely than men in those positions to prioritize the maintenance

of interpersonal relationships, to tend to the morale and welfare of others, or to show consideration for others—e.g., helping and doing favors for subordinates. Subsequent meta-analyses confirmed these early conclusions (van Engen and Willemsen, 2004). Clearly, many female powerholders show no shortage of care for others, even when some scholars have argued that power can unleash self-serving and often destructive behavior that is insensitive to the needs of other people (e.g., Anderson et al., 2003; Keltner et al., 2003; Van Kleef et al., 2008; Lammers et al., 2012; Rucker and Galinsky, 2016). But what makes female powerholders more interpersonally sensitive than their male counterparts? And what are the consequences of women's tendency to wield power "with a velvet glove" (i.e., in a more prosocial way)?

We posit that the answer to these questions partly lies on gendered patterns of *emotional labor*—which we define as the act of self-regulating one's emotions to respond and attend to *others*' needs and emotions in a manner that advances organizational goals (Hochschild, 1983; Grandey, 2000; Cheung and Tang, 2010). We argue that women in power behave in a more prosocial manner than men because they have a stronger tendency to practice emotional labor. These gender[1] differences have a mixed set of consequences: On the one hand, women's more prosocial use of power can be beneficial for subordinates and organizations. On the other hand, we argue that gendered emotional labor practices can simultaneously create costs for individual powerholders—especially when emotional labor is externally motivated—and undermine gender equality in top leadership positions in multiple ways. Here, we integrate the previously disconnected literatures on emotional labor and the psychology of power to articulate three routes through which this happens. We contribute to existing models of gender and leadership by identifying emotional labor as a key construct that can illuminate why men and women express power differently and why it is more difficult for women to attain and retain powerful roles (Vial et al., 2016).

Power is often defined as the extent to which an individual exerts asymmetric control or influence *over others* (Schmid Mast et al., 2009)—for example, having the authority to issue orders that others must follow, or controlling access to valued resources (Magee and Frasier, 2014)—while also being free *from others*, or having the discretion to operate autonomously, unfettered by the will and needs of other people (Fast et al., 2009; Inesi et al., 2011; Lammers et al., 2016). Ostensibly, then, power runs counter to emotional labor, as the latter prioritizes accommodating the emotions of other people rather than imposing one's own views independently from others (Rucker and Galinsky, 2016). Conversely, we propose that when people in power engage in emotional labor, this practice may foster a more prosocial use of power, one that is considerate of others and that promotes or protects their welfare (Batson, 2012). We contribute to the literature on the psychology of power (e.g., Sassenberg et al., 2014; Sturm and Antonakis, 2015; Tost and Johnson, 2019; Foulk et al., 2020) by identifying emotional labor practices as an important antecedent to prosocial power use—one that can help explain why men and women in high-power roles may behave differently.

We argue that gender differences in emotional labor practices and demands translate into women's more prosocial use of power in at least three ways (**Figure 1**). First, women have a *stronger ability* than men to practice emotional labor (**Figure 1**, *path a*), a skill that underlies the prosocial use of power. Second, women have a *stronger internal motivation* than men to perform emotional labor (**Figure 1**, *path b*), which may lead women to construe power in an interdependent manner that fosters prosocial rather than self-serving behavior. And third, women face *stronger external demands* than men to practice emotional labor (**Figure 1**, *path c*), which constrain powerful women's ability to exercise their authority in self-serving ways. In the sections that follow, we integrate the literatures on emotional labor and the psychology of power to develop a theoretical framework in which we articulate these three pathways connecting emotional labor to female powerholders' prosocial use of power (**Figure 1**, *path g*) as well as positive and negative consequences for individuals, groups, and gender equality at large (**Figure 1**, *paths j-l*). We begin by discussing gender differences in emotional labor and then review research that supports the claim that women are more likely than men to behave in a prosocial way when they occupy high-power roles.

WHAT IS EMOTIONAL LABOR AND WHAT ARE ITS ANTECEDENTS?

A variety of social settings have tacit (and sometimes explicit) norms or "display rules" for what is an acceptable or desirable emotional expression. These norms delineate socially appropriate ways of interacting with others, including whether and to what degree felt emotions should be expressed (Ekman and Friesen, 1975; Matsumoto, 1990). At its core, emotional labor is the regulation of felt and expressed emotions (whether effortful or not) to match these emotional display rules with the objective of fulfilling organizational goals (Hochschild, 1983; Grandey, 2000; Cheung and Tang, 2010). People practice emotion regulation in a wide variety of contexts (e.g., students at school, spouses at home; Gross, 1998); however, *emotional labor* specifically occurs when people deploy emotion regulation strategies to meet organizational goals (Grandey, 2000). For example, when an employee in a service job continues to smile to an angry customer to prevent them from leaving the establishment, or when an employee masks their feelings of frustration during a long staff meeting to preserve harmony within the team. Indeed, emotional labor has tangible organizational benefits, as it fosters an atmosphere in which people feel at ease, valued, and understood (Iszatt-White, 2009).

Emotional labor is enacted on two different levels. One of these levels is strictly *intrapersonal* and involves self-regulation and

[1]Throughout this article, we use the term *gender* to refer to the behavioral, social, and psychological characteristics of women and men (as well as norms and expectations about them), which are frequently associated with the biological categories of female and male (e.g., Deaux, 1985; Pryzgoda and Chrisler, 2000). We favor the term *gender* over the term *sex* in our writing because, although it is impossible to fully know the extent of biological and environmental influences on human behavior, the term *gender* has more inclusive implications than the term *sex* (Frieze and Chrisler, 2011).

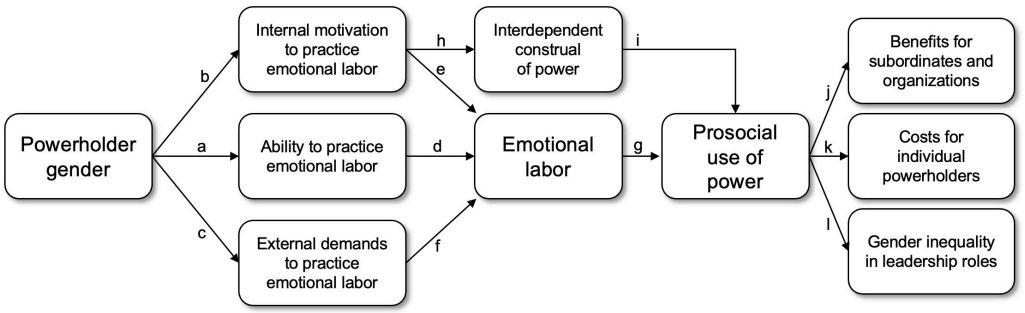

FIGURE 1 | Theoretical model connecting gendered patterns of emotional labor with the prosocial use of power and its downstream consequences. Powerholder gender is related to differences in the ability (*path a*) and the internal motivation (*path b*) to practice emotional labor, as well as in external emotional labor demands (*path c*). These three factors directly contribute to emotional labor (*paths d–f*), which underlies the prosocial use of power (*path g*). Additionally, a stronger internal motivation to practice emotional labor is associated with a more interdependent construal of power (*path h*), which influences the tendency to enact power in prosocial ways (*path i*). The prosocial use of power has benefits for subordinates and organizations (*path j*), but it can also create costs for individual powerholders (*path k*) and undermine gender equality in leadership roles (*path l*).

expression of the right kind and amount of emotion (Totterdell and Holman, 2003; Hülsheger and Schewe, 2011). To achieve this, individuals resort to one of two strategies: (a) a response-focused emotion regulation strategy known as "surface acting," which entails the suppression of felt negative emotions through the modification of facial displays (e.g., "putting on a smiley face"); and (b) an antecedent-focused emotion regulation strategy known as "deep acting" that involves changing inner feelings through cognitive reappraisal—for example focusing on positive rather than negative feelings (Hochschild, 1983; Grandey, 2000, 2003; Cheung and Tang, 2010). In addition to these intrapersonal processes, emotional labor is enacted on an *interpersonal* level. In order to respond adequately to the emotions of another person, one must first identify how that person is feeling (Ashtar et al., 2021). Thus, although an important part of the process is self-oriented, emotional labor is inherently other-oriented as it requires one to be attuned to others' emotions and to accommodate and cater to those emotions (i.e., paying attention to, accurately recognizing, and responding effectively to the feelings of others). Interpersonal and intrapersonal processes can take place sequentially and repeat several times in the course of a single interaction (e.g., identify another person's feelings; self-regulate one's own emotions; produce the appropriate response; identify the person's reaction; recalibrate or maintain one's emotional expression, and so on).

When individuals practice emotional labor (e.g., by being attentive to the emotional experience of others and by self-regulating to respond to those emotions in a way that facilitates organizational goals), such practices can manifest in an interdependent and relational approach and in a wide variety of behaviors. These behaviors, which essentially grease the wheels of human interaction in organizational settings, can be classified into three broad categories, including (a) acting in prosocial rather than self-serving ways (e.g., being interpersonally helpful; showing concern for others' welfare at work; guiding, comforting, and defending others); (b) being sensitive to others' views (e.g., seeking out their opinion; allowing them to voice opposing perspectives; accommodating others' needs); and (c) maintaining a positive emotional environment (e.g., making others feel at ease and valued; tending to their morale; providing them with emotional support).[2]

Antecedents of Emotional Labor: Ability and Motivation

When considering the psychological antecedents of emotional labor, it is important to distinguish between the ability to practice it (**Figure 1**, *path a*) and the motivation to engage in it (**Figure 1**, *path b* and *path c*). One may be skilled at practicing emotional labor but not be particularly motivated to do so—either generally or in a specific context. Alternatively, one may desire to engage in emotional labor and fail miserably. This distinction is key to understanding how emotional labor practices relate to gender, as research suggests that women may be more skilled at behaviors relevant to emotional labor than men as well as more strongly motivated to practice them. Similarly, it is crucial to distinguish between emotional labor that springs from internal motivation (**Figure 1**, *path b*) and emotional labor that is externally motivated (**Figure 1**, *path c*): Whether one genuinely wishes to cater to others' emotions (for instance, out of an *empathic concern* for others; Batson, 1987, 2011), or whether one feels an external demand to do so (e.g., due to formal work-role requirements; Hochschild, 1983; Grandey, 2000; Cheung and Tang, 2010).

These distinctions between ability, internal, and external motivation form the basis of three different routes in our theoretical model through which gender differences in emotional labor result in women's stronger prosocial use of power. According to social role theory (Wood and Eagly, 2002; Eagly and Wood, 2012), gender differences and similarities in social behavior are the product of the disparate distribution of women and men into distinct social roles. For instance, women occupy

[2]Emotional labor practices can be combined with the unique behavioral affordances of high-power roles, manifesting in leadership styles that are more interpersonally oriented, as we explain in the section on *Emotional Labor at the Top of the Hierarchy: Women's Prosocial Use of Power.*

the great majority of care-oriented roles in society. Such gendered distribution of labor, which is due in part to evolved physical differences between women and men (e.g., in terms of size, strength, reproductive activities), influences their behavior through various processes, including the creation of gender roles. These gender roles dictate different expectations for women and men—for example, the kinds of psychological characteristics they are believed to possess. Given that women tend to occupy care-oriented roles, they are expected to possess the psychological characteristics that are best suited to those roles, such as being highly communal, kind, cooperative, etc. These expectations, as well as the requirements of the specific roles that women and men occupy, shape their social behavior (see Eagly et al., 2000) via hormonal processes, socialization practices (i.e., how women and men are taught to behave from a young age), and social regulation (e.g., penalties and rewards for behaving in ways that contradict or uphold expectations, respectively). As we discuss below, gender differences have been identified in the ability, internal motivation, and external demands to practice emotional labor, which reflect the influence of gendered social roles (Wood and Eagly, 2002; Eagly and Wood, 2012).

Gender Differences in Ability to Practice Emotional Labor

Some evidence suggests that women may be more adept than men at the intrapersonal processes entailed in emotional labor practices, as they usually engage in a wider range of emotion regulation strategies than men (Garnefski et al., 2004). For instance, fMRI studies indicate that they use positive emotions in the service of reappraising negative emotions to a greater degree (McRae et al., 2008). With regards to the more interpersonal aspects of emotional labor, studies indicate that women possess better *empathic accuracy* than men—the ability to correctly infer what another person is thinking or feeling (Ickes et al., 2000). Women are also more successful than men at deciphering others' non-verbal cues (La France et al., 2009; Williams et al., 2009), and at recalling people's non-verbal cues and facial expressions (Hall et al., 2007). Other research has revealed that women score higher than men on interpersonal aspects of emotional intelligence, which involves the ability to perceive and express emotion and regulate emotion in the self and others (Mayer et al., 1999), including social skills such as being perceptive, empathic, and adaptable (Argyle, 1994; Petrides and Furnham, 2000; Joseph and Newman, 2010; Cabello et al., 2016).

In sum, empirical evidence indicates that women may be more skilled than men at a host of behaviors that constitute the building blocks of emotional labor. In line with social role theory (Wood and Eagly, 2002; Eagly and Wood, 2012), these ability differences may reflect women's historical tendency to occupy positions in which emotional skills are paramount (e.g., care-oriented roles). As care-oriented roles promote and require emotional abilities, such abilities may become entrenched into the female gender role in a way that shapes women's behavior (Eagly et al., 2000). For instance, the socialization of young girls may place a stronger emphasis than that of boys on the development of emotional skills such as being able to identify and name emotions (McClure, 2000; Brody and Hall, 2010).

However, as alluded to earlier, an ability to practice emotional labor successfully should not be confused with a motivation to do so. This distinction becomes particularly important when considering emotional labor practices that are externally motivated (as discussed below), because ability and motivation in this case may have opposite effects on well-being. Specifically, whereas being more adept at managing emotions could make emotional labor feel effortless, a strong external pressure to do so may take a psychological toll, reducing emotional autonomy and feelings of authenticity (Brotheridge and Grandey, 2002). We discuss these burdens in detail in the section on *The Downstream Consequences of Women's Prosocial Use of Power*.

Gender Differences in Internal Motivation to Practice Emotional Labor

Both internal (i.e., intrinsic) and external (i.e., extrinsic) motivation to practice emotional labor to achieve organizational goals may be stronger in women than in men. With regards to internal motivation, women may genuinely have a stronger proclivity than men to both consider and accommodate the emotions of others. For example, women appear to care more than men about correctly reading and responding to others' emotions (Ickes et al., 2000; Klein and Hodges, 2001). Women are also generally more likely than men to engage in the kinds of non-verbal behaviors that facilitate social interaction (for a review, see LaFrance and Vial, 2016), such as smiling (LaFrance et al., 2003), maintaining eye contact (Hall, 1984); keeping closer physical proximity (Hall and Gunnery, 2013); orienting their body more directly toward their interaction partners (Helweg-Larsen et al., 2004); employing *affiliative speech*, or language that affirms and shows support to the other person (Leaper and Ayres, 2007); and using back-channel responses (e.g., head nodding) to signal that they are listening (Leaper and Robnett, 2011). Other research suggests that women (but not men) may generally internalize prosocial rather than self-interested behavior as their intuitive response to other people (Rand et al., 2016).

As discussed in the previous sections when describing the basic tenets of social role theory (Wood and Eagly, 2002; Eagly and Wood, 2012), although the origins of these gender differences are likely multiply determined, one clear source can be found in different socialization practices that, from a young age, encourage girls more so than boys to cultivate communal attributes (Brody, 1993; Hibbard and Buhrmester, 1998; Shields, 2002; Chaplin et al., 2005). Women consistently report a stronger communal self-concept than men, viewing themselves as friendlier, less selfish, and more concerned with others (e.g., Witt and Wood, 2010; Hsu et al., 2021). Thus, the evidence indicates that women are more highly internally motivated than men to practice emotional labor.

Gender Differences in External Emotional Labor Demands

In addition to having stronger internal motivation, women may also experience stronger external pressures than men to get emotional labor right. Whereas some individuals may be more adept at emotional labor than others and/or personally more inclined to practice it, organizational norms often impinge on

people's ability to express their emotions freely. Indeed, one strong antecedent to emotional labor is the extent to which there are contextual pressures that create a sense of obligation to practice it, or *emotional labor demands*. Organizational contexts and roles vary in how much emotional labor they require. Women are generally more likely than men to hold jobs entailing high work-role demands to display positive emotions either to customers and clients or to coworkers and superiors (Guy and Newman, 2004; Cortes and Pan, 2018). In many female-dominated (i.e., "pink collar") occupations, workers are expected to employ emotional skills to bring about organizational ends, whereas workers in male-dominated occupations do not face these demands (Meier et al., 2006; Johnson and Spector, 2007; Nixon, 2009). Indeed, the concept of emotional labor was originally developed by Hochschild (1983) to describe the experience of low-level service jobs (e.g., flight attendants, customer-oriented roles), which do not offer much opportunity for advancement up the organizational hierarchy, and which continue to be occupied primarily by women (U.S. Bureau of Labor Statistics, 2021).

Importantly, not only are women more likely than men to work in occupations with strong emotional labor demands; they are also more likely than men to encounter pressures to practice emotional labor even when occupying the same organizational roles (e.g., Schaubroeck and Jones, 2000). From the perspective of social role theory (Wood and Eagly, 2002; Eagly and Wood, 2012), cultural gender stereotypes develop from observation of the historical distribution of women and men into different social roles, leading people to *expect and require* women to accommodate others' needs and emotions to a greater extent than men. Indeed, there is a strong belief that women, more so than men, tend to care about and be sensitive to the feelings of other people (Prentice and Carranza, 2002; White and Gardner, 2009; Haines et al., 2016). Stereotypes around emotion expression in particular portray women as well-suited to comply with emotional display rules that require gauging and responding to others' emotions (Lopez-Zafra and Gartzia, 2014) and expressing positivity and interpersonal sensitivity (Shields, 2002; Timmers et al., 2003; Fischbach et al., 2015). People tend to implicitly associate the expression of anger with men (Bijlstra et al., 2010; Neel et al., 2012; Smith et al., 2015); indeed, men are commonly stereotyped as aggressive or violent (Leach et al., 2017) and as more likely than women to display negative emotions such as anger and hostility (Plant et al., 2000; Shields, 2000)—behaviors that are incompatible with emotional labor practices.

Gender stereotypes have a strong prescriptive component (Burgess and Borgida, 1999; Prentice and Carranza, 2002). Thus, people typically think that women *should* be caring, kind, and careful with others' emotions. They do not require the same of men, who are held to a lower communality standard in general (Biernat and Manis, 1994; see also Vial and Cimpian, 2020, for a review of shifting gender standards and social rewards). Unsurprisingly, then, women are judged in relation to a higher standard than men with respect to performing emotional labor at work. For example, an experiment showed that women do not reap any special rewards for being interpersonally helpful with coworkers, whereas men receive accolades for the same behavior (Heilman and Chen, 2005; see also Farrell and Finkelstein, 2007). Women are expected to show positive emotions in general more than men (Hess et al., 2005) and their emotional expression at work is scrutinized more closely (Smith et al., 2016). In contrast, men's emotional expression is judged based on a relaxed standard: Whereas women elicit penalties from other people when they express anger in a professional context and their anger is viewed as unjustified, men's anger in the same context is seen as acceptable and warranted (Brescoll and Uhlmann, 2008; Barrett and Bliss-Moreau, 2009; see also Raymondie and Steiner, 2021). In sum, even in the same organizational role, women encounter stronger external pressures than men to practice emotional labor, and are punished when they do not heed them—even when they occupy high-power roles (as we elaborate on the section on *The Pressure Route: Emotional Labor Demands Curb Women's Self-Interested Use of Power).*

EMOTIONAL LABOR AT THE TOP OF THE HIERARCHY: WOMEN'S PROSOCIAL USE OF POWER

Individuals practice emotional labor at all levels of the organizational hierarchy. Whereas, in its origins, the concept of emotional labor was focused on workers at lower hierarchical levels (Hochschild, 1983), those at the top of the hierarchy also practice emotional labor—identifying others' emotions and self-regulating their own in order to produce the kind of response that may best achieve their organizational goals. Indeed, emotional labor can be an important part of leadership (e.g., Gardner et al., 2009; Humphrey, 2012). This may be particularly the case for management roles embedded in occupational contexts that have a strong care orientation (e.g., healthcare, early education) in which communal attributes and the capacity to nurture others are viewed as more typical in leaders (Yoder, 2001; Cowgill and Vial, 2022). Unsurprisingly, women are better represented in leadership positions in these organizational contexts compared to non-care-oriented occupations (U.S. Bureau of Labor Statistics, 2021).

Emotional Labor at the Top Translates Into Prosocial Use of Power

Given the unique behavioral affordances of high-level roles (e.g., the prerogative to impose authority over others; Magee and Frasier, 2014), we argue that emotional labor in these roles translates into a more prosocial use of power. By "prosocial use of power," we mean a broad range of actions intended to benefit people in the organizational context other than the powerholder (i.e., behaviors such as helping, comforting, sharing, cooperation, etc.; Batson, 2012), which are supported by emotional labor practices that allow for the accurate detection and accommodation of others' emotional needs. Prosocial attitudes and behaviors are generally valued as key features of effective leaders (e.g., Gerzema and D'Antonio, 2013, 2017; Gartzia and van Knippenberg, 2016). Indeed, promoting cooperative relationships with and among

followers is often highlighted as an important leader function (De Cremer and van Knippenberg, 2002).

At the top of the hierarchy, emotional labor practices may translate into a leadership style that is more interpersonally oriented, one that draws less on dominance to influence others and, as a result, increases positive interpersonal behaviors among subordinates (Humphrey, 2012; Kakkar and Sivanathan, 2021). Emotional labor practices among managers and supervisors manifest in prosocial behaviors toward employees (e.g., helping and doing favors for subordinates), showing sensitivity to their views (e.g., not dominating a team interaction; listening and taking subordinates' concerns into account when making decisions), and seeking to foster a positive, friendly work environment that is psychologically safe (e.g., avoid expressing anger or being too critical or too dominant; showing empathy; promoting cooperative relationships with and among followers). At the same time, those with decision-making power are often expected to self-regulate in order to maintain emotions at bay and keep a cool head to make decisions rationally—for example, to suppress feelings of empathy evoked by a specific individual in order to maximize aggregate outcomes for the group or organization they lead (e.g., Uhlmann et al., 2013). Thus, powerholders' effective emotional labor practices entail walking a fine line between showing sensitivity and empathy and being accommodating, while at the same time not letting emotions cloud their judgment. These actions require those in high-power roles to carefully read others' emotions and manage their own—often involving substantial self-regulation—in the service of effective communication and producing the right state of mind in others (i.e., emotional labor; Humphrey, 2012). All of these practices appear to be more common among high-power women compared to high-power men, as we describe next.

Women Wield Power in More Prosocial Ways Than Men

Whether due to a stronger ability (e.g., Garnefski et al., 2004), internal motivation (e.g., Ickes et al., 2000), or external demand (e.g., Heilman and Chen, 2005), we argue that women's greater likelihood to practice emotional labor results in a more prosocial use of power when they wield it compared to men (**Figure 1**, *path g*). Powerholders who engage in emotional labor practices are often described as *transformational* leaders (Wolfram and Mohr, 2010; Vinkenburg et al., 2011) or as *servant* leaders (Barbuto and Gifford, 2010; Lemoine and Blum, 2021), who enact a communally oriented leadership style in which individual consideration ("seeing" and nurturing followers) is key. Research has consistently found that women are more likely than men to adopt these kinds of interpersonally oriented leadership styles (Eagly and Johnson, 1990; Eagly and Johannesen-Schmidt, 2001). For example, an early study revealed that women showed more concern for others than men even when they occupied high-status organizational roles (Moskowitz et al., 1994). Meta-analytic evidence indicates that women in positions of authority are more likely than men in those positions to prioritize the maintenance of interpersonal relationships, to tend to the morale and welfare of others, or to show consideration for others—e.g., helping and doing favors for subordinates (van Engen and Willemsen, 2004). Other work suggests that women (but not men) in high-power roles are sensitive to other people's views and perspectives, and less likely to dominate team interactions (Brescoll, 2011). Further supporting these trends, a study commissioned by LeanIn.org and McKinsey and Company (Thomas et al., 2021), which included responses from over 65,000 employees in 423 companies in the United States and Canada, revealed that female managers were more likely than male managers to provide emotional support to employees and to help them navigate work-life challenges. In the context of academia, surveys have found that female faculty perform significantly more uncompensated internal service than male faculty, acquiescing to participate in committee-work more often, even when controlling for rank (i.e., tenure; Guarino and Borden, 2017).

Thus, the existing evidence indicates that women behave in more prosocial ways than men when they have power. Nevertheless, it would be helpful for future investigations to examine this possibility more directly as well as the connection with emotional labor practices. Studies may test whether gender differences in emotion self-regulation among male and female powerholders predicts the latter's stronger tendency to behave prosocially. Emotion regulation takes time and effortful control (Grandey, 2000); thus, studies could examine whether gender differences in powerholders' prosocial behavior are eliminated in conditions that might impair emotional labor (e.g., under time constraints or cognitive load). Given that women are more skilled at emotional labor than men (Ickes et al., 2000; Garnefski et al., 2004; McRae et al., 2008; Cabello et al., 2016), future studies could also examine whether female powerholders respond better than male powerholders to emotional labor demands.

Multiple Routes to Gender Differences in the Prosocial Use of Power

We propose that gender differences in the ability (e.g., Garnefski et al., 2004), internal motivation (e.g., Ickes et al., 2000), and external demands (e.g., Heilman and Chen, 2005) to practice emotional labor constitute three distinct pathways or routes through which gendered emotional labor practices and demands result in gender differences in the prosocial use of power. Of these three routes, the "ability" route (**Figure 1**, *paths a, d,* and *g*) is the most straightforward, as we describe below. We also propose that there are two other routes connecting gendered emotional labor practices with the prosocial use of power, which are less obvious but equally (or perhaps even more) influential: a "construal" route (**Figure 1**, *paths b, h,* and *i*) and a "pressure" route (**Figure 1**, *paths c, f,* and *g*).

The Ability Route: Women's Greater Aptitude for Emotional Labor Facilitates the Prosocial Use of Power

The ability route focuses on gender differences in the ability to practice emotional labor (**Figure 1**, *path a*), as previously discussed (Ickes et al., 2000; Garnefski et al., 2004; McRae et al., 2008; Cabello et al., 2016). Such differences in ability may logically underlie gender differences in actual emotional labor (**Figure 1**, *path* d). Specifically, women's greater aptitude

for the skills involved in emotional labor relative to men would enable them to practice it, thereby directly influencing women's prosocial use of power (**Figure 1**, *path g*). Women's superior ability to accurately understand what others are feeling (Ickes et al., 2000) and read their non-verbal expressions (La France et al., 2009; Williams et al., 2009) would make it easier for them to subsequently accommodate their needs (e.g., to display the kind of individualized consideration that is central to transformational leadership styles; Eagly and Johnson, 1990; Eagly and Johannesen-Schmidt, 2001). Supporting this view, studies have found that the ability to perceive and respond to others' emotions is positively related to behaving altruistically toward others (Charbonneau and Nicol, 2002). Thus, women may use power more benevolently than men simply because they are better equipped to practice emotional labor.

The Construal Route: Women's Greater Internal Motivation to Practice Emotional Labor Translates Into a More Benevolent View (and Use) of Power

In addition to directly promoting prosocial behavior by increasing the amount of emotional labor practiced (**Figure 1**, *paths b, e* and *g*), we propose that women's stronger internal motivation than men to perform emotional labor may foster prosocial behavior indirectly through a "construal" route: Due to their internal motivation to practice emotional labor (**Figure 1**, *path b*), women construe power in a more interdependent way than men (**Figure 1**, *path h*), which fosters a prosocial use of power (**Figure 1**, *path i*). Beyond the objective degree of power that a person may have (i.e., how much a person is actually in control of their own and others' fate), how a person *construes* their power is fundamental to understanding how they wield it (Sassenberg et al., 2014; Sturm and Antonakis, 2015; Tost and Johnson, 2019; Foulk et al., 2020). Specifically, power appears to magnify preexisting individual dispositions to be more self-oriented or, conversely, more communally oriented (e.g., Côté et al., 2011; Galinsky et al., 2016). Those with power are highly attuned to features in their environment that can help them achieve their goals (Keltner et al., 2003; Guinote, 2007, 2008), including interpersonal and prosocial goals. When people feel powerful, they are better able to connect with and enact their true selves (Kraus et al., 2011; Kifer et al., 2013). Some may approach power in a more "personalized" way that highlights autonomy and dominance over others, whereas some may approach power in a more "socialized" manner that highlights the powerholder's responsibility to ensure the best possible outcomes for the group at large (Frieze and Boneva, 2001; see also Wang and Sun, 2016).

Prosocial effects ensue when powerholders construe their power in interdependent ways that highlight responsibility for the welfare of others (Overbeck and Park, 2006; Gordon and Chen, 2013; De Wit et al., 2017). When people hold a more interdependent self-construal, they use power benevolently (Howard et al., 2007), and when they have a stronger other-orientation they tend to be fairer in their dealings with others (Blader and Chen, 2012). Powerholders with a stronger need to belong or be accepted tend to downplay their power and yield to the opinions and views of other people (Rios et al., 2015). Other work has shown that power can sometimes increase perspective-taking (Hall et al., 2005, 2007; Schmid Mast et al., 2009). The more the powerholder understands the high-power position as empathic and other-oriented, the more he or she is interpersonally sensitive (Chen et al., 2001; Schmid Mast et al., 2009; Côté et al., 2011; Chin et al., 2013). If the psychological experience of power leads powerholders to behave more in line with their other-oriented or self-oriented dispositions (e.g., Kraus et al., 2011; Foulk et al., 2020), then it is possible that baseline gender differences in the internal motivation to perform emotional labor may persist even when men and women occupy positions of power, and women's propensity to act on such motivation may be enhanced. Indeed, recent investigations provide indirect evidence in line with the idea that women may think of people at the top of the hierarchy as being particularly adept at managing others' emotions—that they may view emotional labor as central to power and leadership (e.g., Vecchio and Boatwright, 2002; Bellou, 2011; Hays, 2013; Collins et al., 2014; Gino et al., 2015).

First, given that power facilitates goal pursuit (Keltner et al., 2003; Guinote, 2007, 2008), women's stronger communal goals (Diekman et al., 2011) and internal motivation to practice emotional labor may translate into a more prosocial use of power in alignment with those goals, whereas men's more agentic goals may result in strong self-oriented behavior. Due to their strong emphasis on connection, interpersonal sensitivity, and the overall tendency to see oneself in a relational manner (Josephs et al., 1992; Cross and Madson, 1997; Witt and Wood, 2010; Hsu et al., 2021), women who acquire power may be overall more attuned to the needs and emotions of others, and willing and emboldened to cater to them. Compared to women, men in power may be more content with the possession of the means to dominate or impose their will onto others (i.e., "being feared"; Hays, 2013), as they generally have a more independent self-construal (Guimond et al., 2006) and tend to self-describe as more dominant and assertive (Prentice and Carranza, 2002; Hentschel et al., 2019). For example, in a series of studies, Gino et al. (2015) found that men were more likely than women to desire a highly dominant type of power, "to have an impact on, control or manage other people, influence other people, or control resources others depend on" (Gino et al., 2015).

Second, women appear to have stronger expectations than men for emotional labor in authority figures, which may mirror their differential approach to wielding power when they have it themselves. To illustrate, a meta-analysis of 69 studies drawing from three different research paradigms testing gender stereotypical perceptions of leaders and authority figures revealed that men tend to construe leadership as more agentic and less communal than women (Koenig et al., 2011). Women more than men tend to view arrogance or being controlling as undesirable characteristics of those in powerful roles, and instead value communal, positive emotional attributes in leaders (Vial and Napier, 2018). Other research has similarly revealed that, compared to men, women expect leaders to be more "people-oriented" (Bellou, 2011) and more relational (Boatwright and Forrest, 2000), and react more positively to leaders who behave more communally (Collins et al., 2014) and who show considerateness toward others (Vecchio and Boatwright, 2002).

Thus, women more than men appear to envision the ideal powerful person as someone who is able to relate in a positive emotional manner to other people and to accommodate their feelings and interests; namely, someone who performs emotional labor. This vision may influence how women themselves wield power, leading to more prosocial behavior in female powerholders than in male powerholders.

The Pressure Route: Emotional Labor Demands Curb Women's Self-Interested Use of Power

Finally, the third and last route is a "pressure" route such that, to some extent, observed gender differences in the prosocial use of power reflect subtly coercive emotional labor demands and looming social threats that impinge on women more strongly than on men (**Figure 1**, *path c*). Specifically, we propose that, although attaining structural power could free individuals to behave in more self-serving ways (Kipnis, 1972; Keltner et al., 2003; Van Kleef et al., 2008), the stronger emotional labor demands imposed on women compared to men (e.g., Heilman and Chen, 2005; Brescoll and Uhlmann, 2008; Barrett and Bliss-Moreau, 2009) do not cease as they accrue power. These demands may effectively constrain powerful women's (but not men's) ability to exercise their authority in self-serving ways, resulting in more prosocial power use.

Women in top roles are often expected to be more emotionally available and more sensitive to others than men in similar roles. For example, Schaubroeck and Jones (2000) showed that, within the same large organization, women perceived a stronger requirement to express positive emotions relative to men, even when position tenure and salary level were kept constant (see also Bellas, 1999). In another study, participants expected female leaders to be particularly more effective than male leaders at "caretaking" leader behaviors such as encouraging, assisting, praising, mentoring, and providing resources to others (Prime et al., 2009). Comparable expectations of caretaking and nurturing behaviors have been documented in the realm of academia, where female professors are subject to stronger emotional labor demands from students than male professors (e.g., to do special favors; El-Alayli et al., 2018). Women more than men are expected to adopt a communally oriented style of leadership focused on nurturing followers that involves listening, showing empathy, and providing emotional support to subordinates, commonly known as "servant leadership" (Barbuto and Gifford, 2010; Lemoine and Blum, 2021). Similarly, people expect women more than men to lead in a "transformational" way (Embry et al., 2008; Vinkenburg et al., 2011; Stempel et al., 2015), a leadership style that includes a strong component of consideration and support for subordinates' needs, preferences, and welfare, and the creation of a friendly work environment that is psychologically safe (Rafferty and Griffin, 2004). At a basic cognitive level, research indicates that people expect feminine-faced leaders to be cooperative and display a prosocial leadership style based on altruism, empathy, and reciprocity, whereas they expect masculine-faced leaders to display a dominant style (Spisak et al., 2012).

Expectations that female leaders perform more emotional labor translate into an unspoken requirement that they *should do so*: In order to be seen as effective leaders, women (but not men) must be interpersonally sensitive—sympathetic, compassionate, understanding, forgiving, helpful. These demands to wield power "with a velvet glove" become sharply apparent in the backlash (i.e., social and economic penalties; Rudman, 1998) that high-power women encounter when they do not accommodate or spare others' feelings. A plethora of studies following role congruity theory (Eagly and Karau, 2002) have demonstrated that female leaders are evaluated negatively when they enact their role in dominant ways—for instance, when they discipline or give negative feedback to subordinates (Sinclair and Kunda, 2000; Atwater et al., 2001; Brett et al., 2005) or when they demand a behavior change in others (Williams and Tiedens, 2016). These dominant behaviors, which are antithetical to emotional labor, lead to a perceived "communality deficit" in female leaders (Heilman and Okimoto, 2007; see also Ma et al., 2022), causing them to be seen as cold and interpersonally hostile (Heilman and Okimoto, 2007). Women (but not men) who lead with a directive style are more likely to receive negative evaluations than women who lead with a democratic style (Eagly et al., 1992), and abusive leadership tends to be penalized more harshly in female than in male leaders (Kim et al., 2021). When emotional labor is not readily apparent in leaders, those leaders fare worse if they are women.

The demands placed on female leaders focus strongly on the intrapersonal emotional labor aspect of *deamplifying* emotion—taming the expression of intense emotions (Matsumoto et al., 2005; Moran et al., 2013). Although research indicates that women and men report feeling most emotions to the same degree (Barrett et al., 1998; Else-Quest et al., 2012), women are stereotyped as *too emotional* and overly sensitive (Fischer, 1993; Shields, 2013; Dolan, 2014), and therefore unable to keep a cool head to make decisions rationally (e.g., Citrin and Roberts, 2004; see Brescoll, 2016, for a review). Thus, the emotional makeup of women is viewed as incompatible with some of the intrapersonal emotional labor requirements of high-level positions (Fischbach et al., 2015), leading to close scrutiny of female powerholders' emotional expression. For example, women in top positions elicit more negative evaluations than men in similar roles for expressing anger (Lewis, 2000; Timmers et al., 2003; Brescoll and Uhlmann, 2008), a highly dominant emotion that is typically off limits for low-power individuals (Plant et al., 2000; Tiedens et al., 2000; Petkanopoulou et al., 2019) as well as powerful women (but tends to be condoned in high-power men). But the demand on powerful women to deamplify emotion for the benefit of others does not only target negative emotions, but all emotions more generally (for reviews, see Brescoll, 2016; Smith et al., 2016). As a result, women in high places walk a fine line, risking backlash from others if they fail to get emotional labor "just right."

Research further suggests that performing emotional labor may allow women to successfully ascend the organizational hierarchy, eschewing the negative reactions they often encounter when they behave in explicitly dominant ways (Williams and Tiedens, 2016). For instance, some studies indicate that women reap more benefits than men from enacting transformational leadership practices, such that the teams they lead perform better (Chen and Shao, 2022). Men are held to a lower standard in

this regard, as evidenced by research showing that men who practice transformational leadership tend to be evaluated as more promotable than women (Hentschel et al., 2018). These findings highlight the persistence of an impression management conundrum for women in top positions (Phelan and Rudman, 2010), and suggest the possibility that emotional labor practices may help women navigate these hurdles. Indeed, to lead and influence others without seeming overly domineering, women in powerful roles usually tame the way they express their power (e.g., Amanatullah and Morris, 2010; Moss-Racusin and Rudman, 2010; Brescoll, 2011; Amanatullah and Tinsley, 2013). Practicing emotional labor as an impression management strategy may result in a more prosocial use of power overall.

THE DOWNSTREAM CONSEQUENCES OF WOMEN'S PROSOCIAL USE OF POWER

Women's higher likelihood than men of engaging in prosocial behaviors when they occupy high-power roles has important consequences on many levels: for individual women, for subordinates who report to female authorities, and for organizations and society as a whole. The *positive* effects of women's more prosocial use of power tend to benefit other people: Those who report to or work directly for them, as well as the organizations or groups in which women's power is embedded. Importantly, a focus on the emotional labor practices that underlie prosocial behavior sheds light on the potential *negative* effects of women's prosocial use of power, which burden individual women. We discuss these positive and negative downstream consequences first; then, we articulate how powerful women's emotional labor practices may contribute to gender inequality in organizational hierarchies.

The Positive Effects of Powerful Women's Prosocial Behavior

Women's more prosocial use of power is likely to confer many benefits for subordinates and organizations (**Figure 1**, *path j*). When those in powerful positions are interpersonally sensitive, subordinates directly reap the benefits—for example by being able to influence the decision-making process (De Wit et al., 2017). Organizations as a whole may benefit as well, as emotional labor is central to some of the key aspects of transformational leadership, like individualized consideration (Bass et al., 2003; Byrne et al., 2014), and it could foster a more socially responsible use of power (e.g., Chen et al., 2001). Similarly, in the context of political power and leadership, research has found that politicians' tendency to practice emotional labor (for example, by employing courteous speech and avoiding incivility in debates) can be highly beneficial, reducing political polarization and increasing trust in politicians (Skytte, 2021).

For these reasons, women's higher tendency than men to behave prosocially when they occupy high-power roles may confer important advantages on the people they lead and the organizations in which their power is embedded. Indeed, gender differences in leadership effectiveness tend to favor women over men (Eagly and Carli, 2003; Eagly et al., 2014; Offermann and Foley, 2020). Employee well-being tends to be higher in companies with more women in top positions (Thomas et al., 2021), and teams led by women tend to report more cohesion and cooperation (Post, 2015). Other research suggests that firms with more women in high-power roles are less likely to face discrimination lawsuits (Abebe and Dadanlar, 2021), have better financial performance (Glass and Cook, 2018; Hoobler et al., 2018), and engage in more socially responsible practices (e.g., Glass et al., 2016). In the political realm, a higher proportion of women in parliaments is associated with lower levels of corruption at the country level (Dollar et al., 2001; Swamy et al., 2001; Rivas, 2013). Although some of these findings may rely on observational data, raising the possibility of reverse causality, they converge with experimental studies that suggest a causal relationship. To illustrate, in a series of experiments, the mere presence of a female leader relative to a male leader caused people to anticipate fairer treatment within an organization and better personal outcomes because they associated stronger communal values in the organization when women occupied leadership roles (Joshi and Diekman, 2021). Similarly, when a hypothetical organization was in crisis, participants in two experiments were more likely to trust the organization (e.g., be willing to invest in it) when it was led by women than by men because they expected women to be more skilled at interpersonal emotion management (Post et al., 2019).

We argue that these advantages and benefits may stem from female leaders' greater tendency to use their power in prosocial ways, and that male leaders (and the organizations that they lead) would also generally benefit from practicing more emotional labor. Regardless of their gender, powerholders who practice emotional labor can foster an environment in which employees and subordinates feel supported, are happier, and perform better (Thomas et al., 2021). Thus, although our focus in this article has been on the high standard for emotional labor against which female leaders are judged compared to male leaders (which is arguably unfair), perhaps a greater focus should be placed on identifying ways of increasing emotional labor among male leaders. Indeed, recent research indicates that both male and female leaders can enhance their effectiveness by enacting more communal behaviors that foster cooperation and trust (e.g., Gartzia and van Knippenberg, 2016; Hentschel et al., 2018; Gartzia and Baniandrés, 2019; Post et al., 2019). As more women attain high-power roles, their tendency to practice emotional labor might promote a shift in people's implicit notions of leadership toward valuing communality as a central rather than peripheral aspect (Vial and Napier, 2018), one equally expected and rewarded in all leaders regardless of their gender.

The Negative Effects of Powerful Women's Prosocial Behavior

Whereas powerful women's emotional labor tends to benefit other people, we propose that practicing emotional labor also entails costs for individual powerholders (**Figure 1**, *path k*).

Although women may be socialized to practice emotional labor more than men (Brody, 1993; Hibbard and Buhrmester, 1998; Shields, 2002; Chaplin et al., 2005) and may come to develop stronger emotional abilities than men (e.g., Ickes et al., 2000; Cabello et al., 2016), they may still experience the added external demand to practice emotional labor as a burden. If women in power are interpersonally sensitive because they genuinely care for others (i.e., due to an internal motivation to behave in prosocial ways), then they might feel authentic and experience a higher sense of well-being than when they lack power (Kifer et al., 2013), due to an enhanced felt ability to fulfill their communal goals (Keltner et al., 2003; Guinote, 2007, 2008; Diekman et al., 2011). However, to the extent that women in power feel *pressured* to perform emotional labor (i.e., when they do so to avoid penalties for behaving too dominantly; Phelan and Rudman, 2010), emotional labor may take a psychological toll and detract from their well-being, making the exercise of power exhausting and emotionally draining for women.

Caring for other people can be burdensome in general. Other-oriented emotions such as empathy and compassion (i.e., the emotions that underlie prosocial behavior; Batson, 2011) are cognitively costly and effortful, and people tend to avoid feeling these emotions when given the chance (Cameron and Payne, 2011; Cameron et al., 2019; Scheffer et al., 2021). More specifically, research has documented how emotional labor can be psychologically costly for those who practice it: The purposeful self-control and the suppression of felt emotions that are often involved in the more intrapersonal aspects of emotional labor (Grandey, 2000) have been linked with intensified negative feelings (Scott and Barnes, 2011); emotional dissonance (Hopp et al., 2010); a reduced sense of authenticity (Brotheridge and Grandey, 2002); impaired memory (Richards and Gross, 2000); diminished task performance (Hülsheger and Schewe, 2011); reduced job satisfaction (Judge et al., 2009; Cheung and Tang, 2010); worsened mental health stemming from emotional exhaustion, stress, and burnout (Grandey, 2000; Brotheridge and Grandey, 2002; Beal et al., 2006; Johnson and Spector, 2007); and physical illness, including high blood pressure and cancer (Grandey, 2000; Johnson and Spector, 2007; Hopp et al., 2010).

As this litany suggests, if female powerholders perform more emotional labor than their male counterparts, then they may also fail to realize some of the benefits that power is supposed to bestow on well-being (Kifer et al., 2013). Indeed, women leaders are more likely to be exhausted and chronically stressed than men in similar positions (Thomas et al., 2021). A recent study further revealed that moving up in organizational rank was associated with greater emotional benefits for men than for women—i.e., diminished negative feelings of frustration and discouragement (Taylor et al., 2021). Other research indicates that, compared to men, women anticipate a higher burden of responsibility from attaining a high-power position as well as other negative outcomes (e.g., stronger stress and anxiety; Gino et al., 2015). It is possible that these negative effects may be countered by a sense of fulfillment or personal reward when emotional labor is internally motivated; however, if strong expectations for powerful women to be prosocial create an added pressure for them to engage in emotional labor, the evidence suggests that women will pay a psychological and physical toll.

IMPLICATIONS FOR GENDER EQUALITY AT THE TOP OF THE HIERARCHY

In addition to the potential negative costs for individual women that we discussed in the previous section, emotional labor practices can create an uneven playing field that can contribute to gender inequality in organizational hierarchies (**Figure 1**, *path l*). Women continue to be greatly underrepresented in high-power roles (Eagly and Heilman, 2016; United Nations Women, 2021). Part of this underrepresentation is due to prejudice against women who deviate from the traditional gender role (Heilman and Eagly, 2008). For example, as mentioned earlier, there is strong evidence that women in roles of authority face more careful scrutiny than their male counterparts (Brescoll and Uhlmann, 2008; Barrett and Bliss-Moreau, 2009). But in addition to this prejudice, we argue that women's stronger internal motivation to practice emotional labor, as well as the stronger external demands to do so that they experience relative to men, may undermine their likelihood of actually attaining and retaining power—helping maintain the unequal distribution of men and women in leadership roles.

Channeling Women Toward Less Prestigious Leader Roles

The internal motivation to do emotional labor and enact power more prosocially may keep women from attaining the most prestigious high-level positions. Indeed, women appear more interested in high-power roles when the communal aspects of leadership are emphasized (Schneider et al., 2016; Pate and Fox, 2018; Schneider and Bos, 2019), which makes leadership and femininity appear more congruous (see also Henningsen et al., 2021; and Hentschel et al., 2021). However, such communal attributes are viewed as compatible with leadership primarily in "female-typed" domains such as healthcare or education rather than "male-typed" domains such as technology or finance (Cowgill and Vial, 2022), which tend to be viewed as much more prestigious and to be valued more (Block et al., 2018). Moreover, emotional labor practices may hinder women's advancement up the management ladder, getting them stuck in mid-levels (e.g., International Labour Office, Bureau for Employers' Activities, 2019; Einarsdottir et al., 2018). Emotional labor and prosocial work take up leaders' finite time and energy resources, but are often "invisible" and not usually rewarded in formal ways in organizational contexts (Steinberg, 1999; Guy and Newman, 2004; Bolino and Grant, 2016). Relational service work in academia (e.g., mentoring or doing special favors for students), which female faculty tend to perform at higher rates than male faculty (Tunguz, 2016; Guarino and Borden, 2017; Hanasono et al., 2018; Berheide et al., 2022), is a chief example of the draining effects of such (invisible) emotional labor: Such work takes limited time away from other activities (e.g., research) that are valued much more highly in promotion and tenure decisions. Indeed, experiments show that women are more likely

to volunteer for, be asked to perform, and accept requests to do "low-promotability" tasks that benefit organizations but are unlikely to impact career advancement into more senior leadership roles (Babcock et al., 2017). Thus, emotional labor practices may promote gender segregation *within* leadership, feeding a two-tier system in which male managers are at the top and female managers are at the bottom.

Discouraging Women From Pursuing Top Roles

By making the psychological experience of power overall less appealing for women, the stronger emotional labor demands that women face could discourage them from pursuing high-power roles, ultimately maintaining male dominance in these roles. Again, the difference between internal and external motivation becomes crucial to understanding this nuanced distinction: Whereas women may be intrinsically drawn to high-power roles in contexts that favor communal behavior (Schneider et al., 2016; Pate and Fox, 2018; Schneider and Bos, 2019), they may nevertheless resent the strong external pressure to practice emotional labor around the clock. Research suggests that power is most appealing when it is construed in terms of personal opportunities, and less so when it is construed in terms of responsibility toward others (Sassenberg et al., 2014). If women, relative to men, construe power in a way that entails less autonomy and more responsibility for others, and if women in power experience stronger demands to toe a fine emotional line when dealing with others, these added burdens may partly explain why women are less interested than men in high-power roles. Women may see power as more of a "chore" than men—and rightly so, based on what can be gleaned from the literature on women's experiences with high power roles (e.g., Brescoll, 2016; Thomas et al., 2021). Power, saddled by strict emotional labor demands, may not be an attractive prospect.

Pushing Women to Opt Out of High-Power Roles

In addition to making power less appealing to women or guiding women toward less prestigious high-level roles, emotional labor can further undermine gender equality by making it difficult for women to retain their power. Even when they attain a high-power role, emotional labor makes exercising that power more exhausting and personally draining for women than for men, which may encourage them to give up or opt out of these roles. As reviewed earlier, emotional labor is costly both psychologically (Richards and Gross, 2000; Brotheridge and Grandey, 2002; Beal et al., 2006; Hopp et al., 2010; Scott and Barnes, 2011) and physically (Grandey, 2000; Johnson and Spector, 2007; Hopp et al., 2010), and has a negative impact on work-related outcomes such as performance and job satisfaction (Judge et al., 2009; Cheung and Tang, 2010; Hülsheger and Schewe, 2011). Qualitative studies have revealed that the difficult task of expressing one's authentic self while acquiescing to external expectations to perform emotional labor may drive women to opt out of leadership positions (Frkal and Criscione-Naylor, 2020). Additional research is needed to provide quantitative data to support these findings and to further examine the mechanisms through which emotional labor demands push women out of high-power roles, promoting gender segregation at the top of organizations.

Making Women's Power More Precarious

Beyond the possibility that emotional labor demands may push women out of high-power roles, practicing emotional labor could make power more precarious, putting women at risk of losing it. One reason why women with power cannot simply ignore emotional labor demands from others is that the legitimacy of their power—the extent to which others feel that women deserve to be heeded as authorities—is usually in question (Vial et al., 2016). Even when they occupy a formal position in an organizational hierarchy that confers them with structural power and control over resources, it is more difficult for female authority figures than it is for men in the same positions to elicit status (i.e., respect, admiration, acceptance from others; Magee and Frasier, 2014). These status attributions are key to imbuing power with the kind of legitimacy that fosters cooperation from subordinates and followers (Tyler, 2002, 2006; Levi et al., 2009; Magee and Frasier, 2014). For female powerholders, foregoing emotional labor seems like a steadfast way to lose legitimacy in the eyes of others and, in turn, to be undermined and questioned (Butler and Geis, 1990; Koch, 2005).

Additionally, emotional labor demands may create a catch-22 for women. When they heed such demands, women may run the risk of having their power contested by being seen as inauthentic (Gardner et al., 2009) or too tentative (Forsyth et al., 1997; Bongiorno et al., 2014; Nandkeolyar et al., 2022). The strong communality implicitly conveyed by emotional labor may be seen as more suitable for the follower role than the leader role (Braun et al., 2017). Thus, women in high-power roles who engage in emotional labor may sometimes lose credibility as leaders, especially among male subordinates (Embry et al., 2008; Bongiorno et al., 2014) who have a stronger preference than female subordinates for dominant leaders (Koenig et al., 2011; Vial and Napier, 2018), and who overall appear less supportive of female leaders (e.g., Netchaeva et al., 2015; Vial et al., 2018). These inequalities in leader support contribute to gender segregation at the top of organizations.

Finally, expectations that women will practice emotional labor to a higher extent when they become leaders may result in them being appointed to highly precarious high-power roles—a phenomenon known as the "Glass Cliff" (Ryan and Haslam, 2005, 2007; Glass and Cook, 2016; Morgenroth et al., 2020). Emotional labor (e.g., responding to and managing others' negative emotions) and a prosocial use of power (i.e., an interpersonally oriented leadership style) may be particularly relevant in crisis situations, making people more likely to support and promote women into high-level roles that are risky and uncertain (Ryan et al., 2011; Gartzia et al., 2012). These precarious appointments, however, can set female leaders up for failure—which may subsequently negatively impact the prospects of other aspiring women leaders. For example, Manzi and Heilman (2021) showed in a series of experiments that participants were less likely

to appoint a female candidate to replace an unsuccessful female leader, whereas male candidates were judged independently from the previous leader's performance. Thus, by encouraging the promotion of women into high-risk leadership positions, emotional labor demands and expectations may help maintain gender inequality in executive roles.

CONCLUSION

Research indicates that women wield power in more prosocial, interpersonally sensitive ways than men. We propose that a focus on emotional labor can illuminate why men and women express power differently. The current review highlights multiple routes through which emotional labor practices underlie this gender difference, focusing on women's stronger ability, internal motivation, and external demands to practice emotional labor. By distinguishing among these different routes, we shed light on the disparate consequences of women's more prosocial use of power. Although it has benefits for other people, it also represents an important burden for women themselves—especially when it is motivated by external demands and the prospect of backlash. The stronger emotional labor demands placed on high-power women relative to high-power men can create an uneven playing field, helping explain why women continue to be sorely underrepresented in high-power roles.

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AUTHOR CONTRIBUTIONS

AV conceptualized and wrote the first draft of the manuscript. CC contributed to the literature review and manuscript revision. Both authors approved the submitted version.

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The Island of Female Power? Intersexual Dominance Relationships in the Lemurs of Madagascar

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The extant primates of Madagascar (Lemuriformes) represent the endpoints of an adaptive radiation following a single colonization event more than 50 million years ago. They have since evolved a diversity of life history traits, ecological adaptations and social systems that rivals that of all other living primates combined. Their social systems are characterized by a unique combination of traits, including the ability of adult females to dominate adult males. In fact, there is no other group of mammals in which female dominance is so widespread. Yet, recent research has indicated that there is more interspecific variation in lemur intersexual relationships than previously acknowledged. Here, we therefore review and summarize the relevant literature, quantifying the extent of sex-bias in intersexual dominance relations documented in observational and experimental studies in captivity and the wild. Female dominance is often, but not always, implemented by spontaneous male submission in the absence of female aggression and linked to female sexual maturation. We connect the available evidence to the hypotheses that have been proposed to explain the evolution of female dominance among lemurs. The occurrence of female dominance in all lemur families and the interspecific variation in its extent indicate that it has evolved soon after lemurs colonized Madagascar – presumably in response to particular ecological challenges – and that it has since been reduced in magnitude independently in some taxa. Our study contributes important comparative information on sex roles from an independent primate radiation and provides general insights into the conditions, opportunities and obstacles in the evolution of female-biased power.

Keywords: female dominance, intersexual relationships, social structure, lemurs, primates

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INTRODUCTION

Repeated interactions among the same two individuals involve various combinations of affinitive, affiliative and agonistic interactions, generating diverse patterns of dyadic social relationships (Hinde, 1976). Agonistic interactions involve the exchange of aggressive and/or submissive acts and signals (Hausfater, 1975). Dyadic agonistic interactions in which only one individual exhibits only submissive behavior are clearly decided and can be used to unanimously determine dominance relationships and hierarchies (Hausfater, 1975; Pereira and Kappeler, 1997); all other

agonistic interactions are undecided. Based on the direction and consistency of decided agonistic interactions, pairs of individuals can establish a dominance relationship between them (Drews, 1993), and the emergent structure resulting from all dyadic dominance relationships among group members can be represented as a dominance hierarchy (Allee, 1938; Landau, 1951; Tibbetts et al., 2022). As in humans, where social hierarchies need not rest exclusively on dominance relations and where group perceptions can be important instead (Redhead and Power, 2022), animals can integrate multiple overlapping social networks of different interaction types (Finn et al., 2019), but it is unknown whether they also navigate multiple social hierarchies, so that their social ranks have been primarily based on dyadic relationships and could also not be determined any other way because inferring the perceptions of bystanders would be extremely challenging to measure. First order intentionality is required from individuals to keep track of all their individual dominance relationships (Gallup, 1998). Experimental evidence indicates that individuals in many group-living species also dispose of second order intentionality, i.e., they are able to infer and monitor dominance relationships between third parties and to adjust their behavior accordingly (Jolly, 1966a; Humphrey, 1976; Cheney and Seyfarth, 1990; Bergman et al., 2003; Range and Noë, 2005). It is therefore meaningful to study the properties, drivers and consequences of dyadic dominance relationships at the group level to characterize the resulting hierarchy as it does not just reflect an artifact of human transposition.

Why two individuals establish a dominance relationship is easily explained if one focuses on its adaptive benefits. Every agonistic interaction is costly, especially in terms of a greater than zero risk of suffering an injury or worse. Even small scratches can develop into dangerous infections, and wound healing can draw energy from other energetic demands for days or weeks (Archie et al., 2012; MacCormick et al., 2012; Archie, 2013). It is therefore always advantageous to minimize the potential costs of fighting for both opponents. Two principal mechanisms are available for this purpose. First, signals of physical strength, agility and other species-specific determinants of fighting ability can be assessed and used to evaluate the potential costs and benefits of an agonistic interaction (Arnott and Elwood, 2009). Second, whenever individuals recognize individual conspecifics and are able to remember the outcome of previous agonistic interactions, an established agonistic asymmetry can be acknowledged by a subordinate by evading a confrontation altogether by an early retreat or by displaying formal signals of submission or by either terminating an interaction with submissive behavior (Reddon et al., 2021). The benefits and the other costs of a dominance relation are always asymmetrical, however, with the dominant enjoying priority of access to resources and mates whenever the features of a resource generate a potential for contest competition (Isbell, 1991; Wrangham et al., 1993; Sterck et al., 1997).

Proximate explanations of why two given individuals establish a dominance relation and how they subsequently maintain it differ accordingly. First, in many cases there is an asymmetry in agonistic power based on physical superiority, aggression, age or motivation that consistently predicts the outcome of dyadic agonistic interactions (Giles et al., 2015; Holekamp and Strauss, 2016; Bonanni et al., 2017; Deniz et al., 2021; Tibbetts et al., 2022). Second, it has been argued that some individuals have greater leverage or power because they control a resource that cannot be taken away by force, and this advantage can also predict the outcome of any given conflict (Young et al., 2017; Lewis, 2018, 2022). Power may be based on fighting ability, but also on knowledge or control over a mating opportunity, making it practically challenging to identify its base, however (Hobson, 2020; Hobson et al., 2021). Third, memories of previous interactions with known individuals can promote a learning effect that leads individuals toward exhibiting submissive behavior – either in response to received aggression or spontaneously – toward certain other conspecifics (Johnsson and Åkerman, 1998; Leimar, 2021). This learning process is further reinforced by the winner-loser effect or other self-organizing social dynamics, according to which winning or losing a fight increases the probability of the same outcome in the next agonistic interaction between the two opponents (Dugatkin, 1997; Hsu and Wolf, 1999; Franz et al., 2015; Lerena et al., 2021; Tibbetts et al., 2022). Finally, in some species, such as spotted hyenas and some catarrhine monkeys, the dominance relationship between two individuals does not exist as a result of prior interactions, but because these species have evolved a convergent social convention of maternal rank inheritance (Walters, 1980; Donabedian and Cords, 2021; Ilany et al., 2021). Accordingly, philopatric matriarchs and their female offspring maintain a life-long dominance hierarchy among matrilines in which the youngest daughter occupies the highest rank just below her mother and the oldest daughter is eventually pushed to the bottom of the within-matriline hierarchy. This system of rank inheritance has the evolutionary benefit of reducing the number of costly fights further because there is no need for an initial establishment of dyadic dominance relationships.

Several types of hierarchies have been reported for various animal societies (Chase et al., 2002). For example, a linear hierarchy is the simplest possibility, but it is unlikely if individuals vary little in agonistic power, and its likelihood decreases with increasing group size (Appleby, 1983). Hierarchies with intransitive relationships are therefore more common (Chase et al., 2002). In some species, there are only one or two individuals that dominate all other group members, whereas no consistent and clear dominance relationships can be discerned among the remaining group members (e.g., in wolves: Mech, 1999). In addition, not all individuals may interact with all others, resulting in various numbers of unresolved relationships. Accordingly, hierarchies in different taxa may differ in their steepness, linearity or other properties (e.g., uncertainty, repeatability), and dyadic relationships within hierarchies may differ in the intensity of aggression, the likelihood of counter-aggression or their conciliatory tendency (de Vries et al., 2006; Sánchez-Tójar et al., 2018; Strauss and Holekamp, 2019; Levy et al., 2020). Importantly, sex plays a key role in structuring hierarchies, because males and females differ in fighting strategies and agonistic power (Pandolfi et al., 2021) and are therefore often not distributed randomly across a dominance hierarchy, whether it is linear or not (Kappeler, 1990a; Smuts and Smuts, 1993; Hemelrijk et al., 2008, 2020). Thus, individuals often cluster within a group's

hierarchy as a function of their sex; in group-living mammals with typically either all or most males outranking all females.

Much of the research on animal hierarchies was conducted on non-human primates. They exhibit a rich diversity of social systems, with stunning variation in group size and composition, kinship structures, mating systems and patterns of (allo-)parental care, providing a rich source for interspecific comparisons in studies of social evolution (Smuts et al., 1987; Kappeler and van Schaik, 2002; Campbell et al., 2010; Mitani et al., 2012; for definitions see Kappeler, 2019). However, what sets the social systems of primates apart from those of other orders of mammals is the diversity and complexity of their social structures, defined as the patterning and nature of social relationships (Silk and Kappeler, 2017). Descriptions of and explanations for the evolution of the diversity of female social relationships have been in the center of socio-ecological research for decades, resulting in a profound understanding of their ecological and phylogenetic determinants, behavioral mechanisms, developmental processes and fitness consequences (Wrangham, 1980; van Schaik and van Hooff, 1983; Sterck et al., 1997; Isbell and Young, 2002; Clutton-Brock and Janson, 2012; Schülke and Ostner, 2012; Thierry, 2013; Strier, 2018; Moscovice et al., 2020). Similarly, the causes and consequences of variation in male–male relationships have been studied in detail (van Hooff and van Schaik, 1994; Alberts, 2012). In contrast, most studies of intersexual interactions focused on functions in the immediate context of reproduction, i.e., mate choice, parental care and infanticide (Fernandez-Duque et al., 2009; Kappeler, 2012a; Lukas and Huchard, 2014; but see e.g., Baniel et al., 2016). Dominance relationships between the sexes, in particular, have not enjoyed the same theoretical and empirical attention as same-sex dominance relations (Muller and Wrangham, 2009; Stumpf et al., 2011; Baniel et al., 2017; Kunz et al., 2021). Because male-biased sexual dimorphism is widespread among mammals (Lindenfors et al., 2007), the ability of males of these species to dominate females was presumably considered an unavoidable side-effect of male physical superiority and greater aggressiveness, and male dominance over females was considered to not require specific attention and explanation (Lewis, 2018).

Yet, the endemic primate radiation of Madagascar (Lemuriformes) offers a remarkable exception to the widespread primate pattern of larger males dominating females (Jolly, 1984; Richard, 1987; Kappeler, 1993; Wright, 1999; Dunham, 2008; Lewis, 2020). Recent research has challenged the long-held assertion that ubiquitous female dominance characterizes all lemur species by revealing considerable interspecific variation in this respect, however. Here, we offer an up-to-date appraisal of the relevant studies and reports of intersexual dominance relationships in lemurs and evaluate existing hypotheses about the evolution of female dominance in light of these new insights.

Today, more than 120 species of lemurs are recognized (Rowe and Myers, 2016). Phylogenetic analyses revealed that they represent the living endpoints of an adaptive radiation following a single successful colonization event of Madagascar more than 50 million years ago (Karanth et al., 2005; Herrera, 2017). Representing only one of four groups of terrestrial mammals that successfully colonized Madagascar (Poux et al., 2005; Kappeler et al., 2019), they subsequently diversified into 5 families and 15 genera plus at least 17 species from 8 additional genera that went extinct within the last few centuries (Godfrey, 2016). This adaptive radiation generated diversity in all fundamental adaptations. Their body sizes span several orders of magnitude (from 30 g – @ 150 kg), and the corresponding life history traits vary accordingly (Catlett et al., 2010). Lemurs evolved diurnal activity at least twice (Santini et al., 2015), and the diversity of their diets matches that of all other primates combined (Richard and Dewar, 1991). Their social systems are equally distinctive, with a wide range of socially diverse solitary species, at least two types of pair-living species, and group-living species in two separate families (Kappeler, 1997, 2012b; Kappeler and Pozzi, 2019). Yet, despite this stunning diversity in fundamental traits, lemurs differ from many better-studied anthropoid primates in that their groups are on average smaller, even after controlling for body size and phylogeny, the average adult sex ratio of their groups is not female-biased, they lack male-biased sexual dimorphism in body and canine size, females have masculinized external genitalia and female dominance is widespread (Richard, 1987; Kappeler and Fichtel, 2015).

Prominent reports of female dominance in ringtailed lemurs (*Lemur catta;* Jolly, 1966b), sifakas (*Propithecus verreauxi* and *P. coquereli*, Richard, 1974) and indris (*Indri indri*, Pollock, 1979), which were the subjects of some of the first extended field studies, contributed to the widespread notion that all lemurs exhibit female dominance (but see Pereira et al., 1990). Being apparently largely confined to lemurs, female dominance never became a mainstream topic in primatology because it appeared to require special explanation and generated several hypotheses that invoked lemur- or Madagascar-specific factors to explain the evolution of this sex role "reversal." However, recent studies revealed several instances where lemur females only win a proportion of agonistic interactions with males, or where females dominate only some, but not all males, and even male dominance has been indicated in one report, suggesting the action of diverse selective forces. Below, we first summarize this variation in detail before we link it to the hypotheses proposed to explain the evolution of female dominance to facilitate the connection of this body of literature to studies of sex-based effects on power, status, dominance and leadership in other mammalian societies that have begun to enter mainstream ethology and primatology as a result of a more general recent interest in sex roles in human and animal societies (Gowaty et al., 2012; Schärer et al., 2012; Janicke et al., 2016).

DIVERSITY OF INTERSEXUAL DOMINANCE RELATIONS

In this section, we summarize the current knowledge about patterns of intersexual dominance relations in all genera of lemurs. We proceed taxonomically (by genus), summarizing relevant details of male–female interactions and relationships, including the proportion of decided conflicts and whether males and females are able to dominate some or all members of the opposite sex. We also note whether studies were observational

or experimental, whether they took place in captivity or the wild, and whether they covered periods of reproduction. To provide context for these details, we also ask whether males and females are permanently associated and report the degree of sexual size dimorphism. The main variables are also summarized in **Table 1**.

Mouse and Dwarf Lemurs (Cheirogaleidae)

Allocebus

No data are available on intersexual conflicts or dominance relationships in the hairy-eared dwarf lemur, ***Allocebus trichotis***, the only member of this genus.

Cheirogaleus

No reports on intersexual conflicts and their outcomes are available for any of the about 10 species of dwarf lemurs in the genus ***Cheirogaleus***.

Microcebus

Among the currently recognized 25 species of mouse lemurs, genus ***Microcebus***, some evidence on the outcomes of intersexual conflicts and dominance relationships is available for 10 species (40%). Among these, direct observational, quantitative data on the outcomes of intersexual conflicts from natural forest environments is only available for two species (*M. berthae, M. griseorufus*). The intersexual conflict behavior of the other eight species was either quantified in captivity (*M. lehilahytsara, M. murinus*) or in wild animals that were observed during social encounter experiments (*M. bongolavensis, M. danfossi, M. mamiratra, M. margotmarshae, M. myoxinus, M. ravelobensis*). For these experiments, one male and one female were temporarily (up to 1 week) kept in one or two connected cages, observed, and subsequently released at their point of capture.

This general scarcity of published, quantitative data for wild mouse lemurs is due to their social organization and difficult observation conditions for these small, arboreal, nocturnal solitary foragers. Social encounters occur only infrequently at night, and the identity as well as sex of the interaction partner cannot always be ascertained, even if some focal animals are equipped with radio-collars. The experimental encounter paradigm solves these problems, since the confinement of two animals to one cage setting increases social interaction rates and eliminates the identification problem. The determination of dominance relationships between two animals is therefore largely facilitated, although potential habituation problems and the confinement to limited space constrain the external validity of the results.

In one field study on ***M. berthae*** (188 h observation time before and during the mating season in Kirindy Forest), females won all (100%) observed conflicts with males, which occurred during feeding and in the sexual context (Dammhahn and Kappeler, 2005). The underlying number of conflicts was low ($n < 10$), however, and no further details were provided. Social encounters in wild *M. berthae* were rare in general (males: 0.93 encounters/h, females: 0.49 encounters/h), but intersexual encounters were more frequent than encounters between females or between males (Dammhahn and Kappeler, 2005).

A study on ***M. griseorufus*** in Berenty Reserve reported a mixed pattern during intersexual conflicts (Génin, 2013). Females won 47% of all observed conflicts with males (n = 34 conflicts). Although adult females were typically able to dominate males, three heavy males were reported to win conflicts with subadult females. In addition, females but not males were able to monopolize fruiting trees, and females fed significantly longer than males at these trees (Génin, 2013).

Outcomes of intersexual conflicts and intersexual dominance were determined in social encounter experiment with six male-female dyads of ***M. bongolavensis*** in Marosely Forest (Evasoa et al., 2019). During 108 observation hours in the non-reproductive season (July – August), females won 80% of all decided conflicts, but conflicts were generally rare (0.35 conflicts/h, $n = 38$), only one of six females was dominant over her male partner, and only 52.6% of all conflicts were decided (Evasoa et al., 2019). In fact, experimental pair partners were relatively often observed in mutual proximity and body contact.

Outcomes of intersexual conflicts and intersexual dominance in six male-female dyads of ***M. danfossi*** were also determined experimentally in Anjiamangirana Forest during 108 observation hours in the reproductive season (September – October). Two females were in estrus, two had recently been in estrus, and one was pregnant during the observations. The overall conflict rate was not very high (0.97 conflicts/h, n = 105). Still, most conflicts were decided (87.6%), females won significantly more conflicts than their male partners, and half of the females were dominant over their temporary mates (Evasoa et al., 2019).

Six male-female dyads of ***M. mamiratra*** were subjected to the same social encounter experiment in Lokobe National Park during the reproductive season (July). One female was swollen, one had been in estrus recently, and one was pregnant during the observations. Overall, conflicts occurred very frequently (8.8 conflicts/h, $n = 954$), significantly more often than in any other species tested with this paradigm, and most conflicts were decided (85.6%). All six females were dominant over their male partner and won 96.7% of all decided conflicts (Evasoa et al., 2019).

Using the same experimental design, six male–female dyads of ***M. margotmarshae*** were observed during the reproductive season (August–September) in Ankaramibe Forest (Evasoa et al., 2019). Two females had recently been in estrus and one female gave birth and lactated during the study. Conflicts occurred frequently (2.7 conflicts/h, $n = 114$) but less often than in their sister species *M. mamiratra*. Three of six females were dominant over their male partner, but one case of male dominance was also observed. Still, females won most decided conflicts (87.6%) and 77.1% of all conflicts were decided.

In ***M. myoxinus,*** the social encounter experiment was conducted in Bombetoka Forest in the non-reproductive season (September – October). Conflicts were generally rare (0.28 conflicts/h, $n = 30$) and intersexual dominance could not be determined in any dyad (Evasoa et al., 2019). Females still won the majority (60%) of all decided conflicts, but most (73.7%) conflicts were undecided. In this species, the authors suspected a high

TABLE 1 | Life style, sexual body mass dimorphism, conflict characteristics, and intersexual dominance relationships in lemurs (Lemuriformes).

Genus	Species	Origin	obs/ exp	hrs	Perm. MF association	Social organization	Season	Sexual dimorphism (body mass, SSD)	Reference SSD	Females can dominate males	Males can dominate females	% decided AIs won by females	% decided AIs	% males subordinate	% females subordinate	Reference dominance
Avahi	*occidentalis*	Wild	obs	847	Yes	Pairs	Both	0.83	1	Yes	No	100	100	100	0	7
Daubentonia	*madagascariensis*	Captive	obs	160	No	Solitary	Non-repro	1.07	1	Yes	Yes	68.0	74.5	N/A	N/A	8
Eulemur	*coronatus*	Captive	obs	N/A	Yes	Group	Repro	1.19	1	Yes	Yes	81.0	83	75.0	25.0	9
Eulemur	*flavifrons*	Captive	obs	260	Yes	Group	Non-repro	0.86	1	Yes	No	98.8	100	100	0	10, 11
Eulemur	*fulvus*	Captive	both	233	Yes	Group	Non-repro	1.07	1	Yes	Yes	< 50	27.7	N/A	N/A	12
Eulemur	*macaco*	Captive	both	260	Yes	Group	Non-repro	0.99	1	Yes	Yes	45.0	46	N/A	N/A	12
Eulemur	*mongoz*	Wild	obs	N/A	Yes	Pairs	Repro	0.88	1	Yes	No	100	100	100	0	13
Eulemur	*rubriventer*	Captive	obs	N/A	Yes	Pairs	Repro	1.05	1	Yes	N/A	88.2	53.1	100	N/A	9
Eulemur	*rufifrons*	Both	obs	200	Yes	Group	Both	0.94	1	Yes	Yes	< 33	33.5	100	100	14
Hapalemur	*alaotrensis*	Wild	obs	> 140	Yes	Group	Non-repro	0.98	1	Yes	Yes	83.0	N/A	N/A	N/A	15
Hapalemur	*griseus*	Both	obs	337	Yes	Pairs	Non-repro	1	1	Yes	Yes	81.0	N/A	100	100	11
Hapalemur	*meridionalis*	Wild	obs	1,762	Yes	Group	Repro	0.96	1	Yes	Yes	> 90	N/A	100	66.7	16
Indri	*indri*	Wild	obs	N/A	Yes	Pairs	Both	0.82	1	Yes	No	100	100	100	0	17
Lemur	*catta*	Both	obs	242.5	Yes	Group	Both	0.98	1	Yes	No	99.5	99.5	100	0	14
Lepilemur	*leucopus*	Wild	obs	516	No	Pairs	Both	0.97	1	Yes	No	100	100	100	0	18
Lepilemur	*ruficaudatus*	Wild	obs	> 2,000	No	Pairs	Both	0.99	1	Yes	Yes	50.3	63.3	100	100	19
Microcebus	*berthae*	Wild	obs	188	No	Solitary	Repro	1.00	1	Yes	No	100	100	N/A	N/A	20
Microcebus	*bongolavensis*	Wild	exp	108	No	Solitary	Non-repro	1.00	2	Yes	No	80.0	52.6	16.7	0	21
Microcebus	*danfossi*	Wild	exp	108	No	Solitary	Repro	0.93	2	Yes	No	91.3	87.6	50.0	0	21
Microcebus	*griseorufus*	Wild	obs	N/A	No	Solitary	Both	0.97	1	Yes	Yes	47.1	N/A	N/A	N/A	22
Microcebus	*lehilahytsara*	Captive	exp	18	No	Solitary	Repro	0.87	3	Yes	Yes	82.4	99.5	62.5	12.5	23
Microcebus	*lehilahytsara*	Captive	exp	20.25	No	Solitary	Non-repro	0.92	3	Yes	Yes	48.0	94.4	33.3	44.4	23
Microcebus	*lehilahytsara*	Captive	obs	N/A	No	Solitary	Repro	1.07	5	Yes	N/A	94.2	86.3	N/A	N/A	24
Microcebus	*mamiratra*	Wild	exp	108	No	Solitary	Repro	0.84	2	Yes	No	96.7	85.6	100	0	21
Microcebus	*margotmarshae*	Wild	exp	108	No	Solitary	Repro	0.87	1	Yes	Yes	87.6	77.1	50.0	16.7	21
Microcebus	*murinus*	Captive	obs	42	Yes	Solitary	Repro	0.84	4	Yes	No	99.9	88.7	100	0	25
Microcebus	*murinus*	Captive	exp	33.75	No	Solitary	Repro	0.84	4	Yes	No	85.3	93.0	53.3	0	23
Microcebus	*murinus*	Captive	exp	29.25	No	Solitary	Non-repro	1.03	3	Yes	Yes	62.2	87.0	23.1	7.1	23
Microcebus	*myoxinus*	Wild	exp	108	No	Solitary	Non-repro	0.86	2	No	No	60.0	26.3	0	0	21
Microcebus	*ravelobensis*	Wild	exp	105	No	Solitary	Non-repro	1.09	1	Yes	No	84.4	58.2	33.3	0	21
Microcebus	*ravelobensis*	Wild	exp	102	No	Solitary	Non-repro	1.09	1	Yes	Yes	48.1	64.6	5.9	11.8	26
Mirza	*zaza*	Captive	obs	N/A	Yes	Pair-living	Repro	0.97	1	No	Yes	N/A	N/A	N/A	N/A	27
Phaner	*pallescens*	Wild	obs	455	Yes	Pair-living	Repro	0.93	6	Yes	No	100	84.0	100	0	28
Prolemur	*simus*	Captive	obs	N/A	Yes	Groups	Both	1.13	1	No	Yes	0	N/A	N/A	N/A	29
Propithecus	*coquereli*	Captive	obs	100	Yes	Groups	No info	1.00	1	Yes	No	100	100	100	0	30
Propithecus	*coronatus*	Wild	obs	273	Yes	Groups	Non-repro	0.86	1	Yes	Yes	80.0	100	50.0	N/A	31

(Continued)

TABLE 1 | (Continued)

Genus	Species	Origin	obs/ exp	hrs	Perm. MF association	Social organization	Season	Sexual dimorphism (body mass, SSD)	Reference SSD	Females can dominate males	Males can dominate females	% decided AIs won by females	% decided AIs	% males subordinate	% females subordinate	Reference dominance
Propithecus	*diadema*	Wild	obs	325	Yes	Groups	Non-repro	0.96	1	Yes	Yes	87.5	100	83.3	16.7	32
Propithecus	*edwardsi*	Wild	obs	14,893	Yes	Groups	Both	1.00	1	Yes	Yes	94.0	100	N/A	N/A	33
Propithecus	*tattersalli*	Captive	obs	4,110	Yes	Groups	Both	1.05	1	Yes	Yes	90.0	100	100	100	34
Propithecus	*verreauxi*	Wild	obs	2,808	Yes	Groups	Both	1.03	1	Yes	Yes	90.8	100	83.3	N/A	35
Propithecus	*verreauxi*	Wild	obs	4,965	Yes	Groups	Both	1.03	1	Yes	Yes	100*	100	100	N/A	36
Varecia	*rubra*	Captive	obs	20	Yes	Groups	Both	0.9	1	Yes	No	100	96.5	100	0	37
Varecia	*variegata*	Both	obs	N/A	Yes	Groups	Both	0.97	1	Yes	No	97.5	76.5	100	0	38

*Origin, place of study; obs, pure observation; exp, encounter experiment with observation; hrs, total hours of observation; perm., permanent; repro, reproductive season; non-repro, non-reproductive season; AIs, agonistic interactions; % males/females subordinate, % males/females who are subordinate towards at least one member of the opposite sex; *, females from an age of 7 years; N/A, not available.*

References: (1) Kappeler et al., 2019; (2) Radespiel et al., 2012; (3) Hohenbrink, 2015; (4) Hohenbrink et al., 2015b; (5) Kappeler et al., 2005; (6) Rowe and Myers, 2016; (7) Ramanankirahina et al., 2011; (8) Rendall, 1993; (9) Marolf et al., 2007; (10) Digby and Kahlenberg, 2002; (11) Digby and Stevens, 2007; (12) Roeder et al., 2002; (13) Curtis and Zaramody, 1999; (14) Pereira and Kappeler, 1997; (15) Waeber and Hemelrijk, 2003; (16) Eppley et al., 2017; (17) Pollock, 1979; (18) Dröscher and Kappeler, 2014; (19) Hilgartner et al., 2012; (20) Dammhahn and Kappeler, 2005; (21) Evasoa et al., 2019; (22) Génin, 2013; (23) Hohenbrink et al., 2016; (24) Jürges et al., 2013; (25) Radespiel and Zimmermann, 2001; (26) Eichmueller et al., 2013; (27) Stanger et al., 1995; (28) Schülke and Kappeler, 2003; (29) Roullet, 2011; (30) Kubzdela et al., 1992; (31) Ramanamisata et al., 2014; (32) Rasolonjatovo and Irwin, 2020; (33) Pochron et al., 2003; (34) Wallace et al., 2016; (35) Kappeler et al., 2009; (36) Voyt et al., 2019; (37) Meyer et al., 1999; (38) Raps and White, 1995.

degree of behavioral disturbance by nocturnal human visitors passing nearby, since the animals were often jointly hiding in the sleeping site during the observation.

Intersexual dominance was also assessed experimentally in ***M. ravelobensis*** in Ampijoroa Forest in two studies during the non-reproductive season (Eichmueller et al., 2013: June – August, Evasoa et al., 2019: May – June). Eichmueller et al. (2013) observed 17 male–female dyads that could each interact only during 6 h of supervised encounter time distributed over four consecutive nights, adding up to a total observation time of 102 h. This study documented 206 intersexual conflicts but found female dominance in only one and male dominance in two out of 17 male–female dyads. This rather low incidence of female dominance coincided with a low rate of winning for females (48.1%) and a low rate of decided conflicts (64.6%), despite a moderately high overall conflict rate (2.0 conflicts/h). Evasoa et al. (2019) observed six male-female dyads for 105 h and detected female dominance in two out of six male-female dyads. Conflict rates (0.52 conflicts/h) and decision rates (58.2% of $n = 55$) were both rather low, but females still won 84.4% of all decided conflicts.

These six mouse lemur species were studied with the exact same experimental paradigm by the same observer, but differed significantly in their levels of mutual tolerance and patterns of intersexual dominance (Evasoa et al., 2019). The multivariate analyses on this multi-species dataset revealed that neither phylogenetic proximity nor habitat type (dry vs. humid forest) could explain the observed interspecific variation in intersexual relationships. However, reproductive activity did coincide with a higher incidence of female dominance, and an impact of seasonal reproduction on the frequency of intersexual conflicts in mouse lemurs was suggested.

Significant seasonal differences in intersexual conflict rates and the outcome of conflicts were also detected in captivity (Hannover colony, Germany) in ***M. lehilahytsara***. Hohenbrink et al. (2016) employed a social encounter paradigm and conducted a series of encounters (=2.25 h/pair) with eight dyads during the reproductive season and with nine dyads during the non-reproductive season. Intersexual conflicts were significantly more frequent in the reproductive season (60.2 conflicts/h, $n = 1{,}084$) than in the non-reproductive season (19.4 conflicts/h, $n = 393$). Although the vast majority of conflicts was decided in both seasons (reproductive season: 99.5%, non-reproductive season: 94.4%), females won relatively more conflicts in the reproductive season (82.4%) than in the non-reproductive season (48%), which was also reflected in the higher proportion of dominant females in the reproductive season (62.5%) than in the non-reproductive season (33.3%). Conversely, males dominated females in four of nine dyads (44.4%) during the non-reproductive season. The seasonal change in dominance from the reproductive to non-reproductive season happened even in individual dyads (1x from female-dominant to male-dominant, 1x from female-dominant to undecided, 1x from undecided to male-dominant).

Another captive study on ***M. lehilahytsara*** was conducted in the Masoala Hall of Zurich Zoo (Switzerland) during 2 months after animals reappeared from seasonal torpor at the start of

the reproductive season (Jürges et al., 2013). Focal animals had relatively frequent social encounters (defined as proximity of < 10 m) with a median of 10 times/h, although the majority of encounters (median = 75%) did not involve social interactions (Jürges et al., 2013). A total of 80 conflicts were observed between males and females in different contexts (feeding, social, sexual, unspecific), the vast majority of them being decided (86.3%, $n = 69$). Females won most decided conflicts (94.2%, $n = 65$), in fact significantly more than males (Jürges, 2010).

A study on agonistic intersexual conflicts and dominance in captive ***M. murinus*** documented unambiguous female dominance (i.e., all females were dominant over all males) in four study groups that were each composed of two adult males and two adult females (Radespiel and Zimmermann, 2001) and were observed for a total of 42 h after group formation during the reproductive season. The study period also included the first seasonal estrus of the females. Overall, 865 agonistic interactions were observed with an overall rate of 20.6 conflicts/h. Most of them were decided (88.7%) and in all but one case in favor of females (99.9%). Intersexual conflicts occurred in various behavioral contexts (sexual, feeding, sleeping, social, spatial).

Significant seasonal differences in intersexual conflict rates and outcomes of conflicts were detected in a more recent study on captive ***M. murinus***. Hohenbrink et al. (2016) studied experimental encounters between 15 dyads during the reproductive season and 13 dyads during the non-reproductive season. Intersexual conflicts were significantly more frequent in the reproductive season (26.9 conflicts/h, $n = 909$) than in the non-reproductive season (5.8 conflicts/h, $n = 169$). The vast majority of conflicts was decided in both seasons (reproductive season: 93%, non-reproductive season: 87%). Females won relatively more decided conflicts in the reproductive season (85.3%) than in the non-reproductive season (62.2%). This seasonal impact was also reflected in the higher proportion of dominant females in the reproductive season (53.3%) compared to the non-reproductive season (23.1%). During the non-reproductive season, one male even dominated his female partner (same dyad: undecided during reproductive season); an outcome that was never observed during the reproductive season. The difference in the proportion of dominant females in both captive studies on *M. murinus* was argued to be the result of the different test paradigms (permanent group formation during estrus vs. temporary encounters outside estrus).

Although many studies have been conducted on wild ***M. murinus*** over the last 60 years, quantitative data on the frequency and outcomes of intersexual conflicts have not been published for this species to the best of our knowledge. However, two studies at Kirindy Forest documented that some females spatially monopolized food resources (in particular gum trees) by chasing males, but not other females, out of gum trees (Génin, 2003, 2013). One additional early study from the reproductive season (September – November) in Ankarafantsika National Park reported that although gray mouse lemurs spent an overall 11% of the observation time within 10m of conspecifics ($n = 195$ encounters), only 11.8% ($n = 23$) of the encounters included aggressive behaviors or "rejections of contact" (Pagès-Feuillade, 1988). Among these, the sex was known for both partners in 18 cases, and 83.3% ($n = 15$) of these occurred between the sexes. During these intersexual conflicts, females mostly rejected contacts attempted by males, suggesting that *M. murinus* females were dominant over males, which may have been facilitated by a female-biased body mass dimorphism (Pagès-Feuillade, 1988).

Mirza

No quantitative data are available on intersexual conflicts or dominance relationships in ***Mirza coquereli***. Only very few data are available on intersexual conflicts in ***Mirza zaza***. One captive study reported on social interactions between one adult male and two adult females at the Duke Lemur Center (Stanger et al., 1995). The authors observed social interactions between the sexes during one estrous cycle of both females, and aggressive behavior was only displayed by the male but not by the females. This observation is suggestive of male dominance, but the lack of systematic data precludes a conclusive assessment.

Phaner

Of the four recognized species of the genus *Phaner*, the social system, including intersexual conflict and dominance, has only been studied in ***Phaner pallescens*** (formerly referred to as *P. furcifer*), which live in family groups comprised of an adult pair and their offspring (Schülke and Kappeler, 2003). This study was conducted in Kirindy Forest and involved 455h of focal observations on 15 male and 15 female pair partners. Agonistic conflicts occurred at relatively low rates (0.49 conflicts/h, $n = 225$) but still more frequently than affiliative interactions. Conflicts occurred mostly in the feeding context (60.4%), but also during mate guarding, meetings with neighbors, resting, and during immigration of a new male (Schülke and Kappeler, 2003). The majority of conflicts (84%, $n = 189$) were decided, and all (100%) were won by females. Submissive behaviors of males occurred spontaneously (i.e., without aggression by females) in more than half of all decided conflicts (55.6%, $n = 105$).

Sportive Lemurs (Lepilemuridae)

Lepilemur

Data on intersexual conflicts and dominance relationships of the 26 species of nocturnal sportive lemurs are available from field studies on only two of them.

Social interactions between eight pairs of redtailed sportive lemurs (***Lepilemur ruficaudatus***) were studied in Kirindy Forest for 24 months (Hilgartner et al., 2012). Due to the nature of their social organization as dispersed pairs, only 255 social encounters between pair partners were observed. Almost half (47.3%) of these encounters involved the exchange of agonistic behavior. Of the 120 agonistic interactions, 63.3% were decided. On average, half (49.7%) of them were won by males, but during the mating season, this rate increased to 87.1% ($n = 31$). In contrast, males lost most of the conflicts (78.9%, $n = 38$) during the birth season. During the rest of the non-mating season, agonistic encounters between pair partner were rare ($n = 7$) and wins were equally distributed between pair partners. Notably, not a single affiliative interaction between pair partners was ever observed.

Twenty nocturnal white-footed sportive lemurs (***L. leucopus***) were observed at Berenty Reserve for a complete annual cycle.

Despite parallel observations of the members of 7 dispersed pairs, only 15 agonistic interactions were observed at all during 516h of focal observations (0.03 conflicts/h) (Dröscher and Kappeler, 2013). Most of them involved unidentified neighbors, and only three agonistic interactions between members of a pair were observed, and in all of them (100%) the female displaced the male from a food patch (Dröscher and Kappeler, 2014).

Thus, in sportive lemurs, rates of (agonistic) interactions are extremely low. They appear to lack unambiguous submissive behavior, contributing to relatively high proportions of undecided conflicts. Sex did not predict the outcome of decided conflicts in *L. ruficaudatus*, except during periods of reproduction. Interestingly, during the mating season males prevailed more often whereas females dominated males when they had small infants. In *L. leucopus*, females appear to be dominant over males, but the sample size is extremely small and agonistic interactions are so rare that dominance may not be a useful concept to describe the outcome of these few interactions.

Aye-Ayes (Daubentoniidae)

Daubentonia

Intersexual dominance relationships in solitary nocturnal aye-aye, ***Daubentonia madagascariensis,*** were studied in a captive colony at the Duke Lemur Center (Rendall, 1993). Two pairs of wild-caught individuals were observed for 160h, but only one of them consisted of adult individuals. Of 55 agonistic interactions between the members of the adult pair, 74.5% were decided, and 68% of the decided (and 42.9% of 14 undecided) conflicts were won by the female. Undecided interactions in this study were defined as those in which one individual exhibited only aggressive behavior, while the other responded with a combination of aggressive and submissive behavior. In the juvenile pair, the male was older, heavier and larger than the female. He managed to elicit submissive behavior by the female in 87% of the decided conflicts (n = 120) between them. However, the young female managed to displace the male in the majority (83.4%) of 66 undecided conflicts, most of which involved access to food. Thus, female aye-ayes appear to be able to dominate males, but larger sample sizes and data on intersexual encounter rates in their very large home ranges of hundreds of hectares (Sefczek et al., 2020) are required to establish the external validity of this preliminary study.

Indris (Indriidae)

Intersexual relationships in the Indriidae have been studied mainly in the course of observational studies in the wild, except for Coquerel's and golden-crowned sifakas (*Propithecus coquereli, P. tattersalli)*.

Avahi

The genus *Avahi* consists of nine species but information on intersexual conflicts is only available for one species, the Western woolly lemur (***Avahi occidentalis)***. Western woolly lemurs are nocturnal and live in cohesive pairs. Six pairs were observed for 847 h over a period of 8 months in the National Park Ankarafantsika (Ramanankirahina et al., 2011). In total, 21 agonistic interactions with a median rate of 0.01/h were observed. Of those conflicts, 15 were decided and 5 were incompletely observed. All 15 decided conflicts between pair partners were won by females and males showed submissive behavior, suggesting that females are dominant over males.

Indri

Indri indri are diurnal and organized into pairs. Three pairs with their offspring were observed over a period of 15 months in Andasibe-Mantadia National Park (Pollock, 1979). In total, 135 social displacement including aggressive displacements were observed in two groups, whereas 107 social displacements – mainly in small feeding trees - were observed in the third group. Adult female indris always displaced adult males, and are, hence, dominant over males.

Propithecus

The genus *Propithecus* consists of nine species, which are all diurnal and group-living. Information on intersexual conflicts is available for six species. Coquerel's sifakas (***P. coquereli***) were observed in outdoor enclosures of the Duke Lemur Center (Kubzdela et al., 1992). Two pairs of an adult female and male were observed for 100 h each outside the reproductive season. In total, 26 aggressive interactions were observed in feeding contexts. Females initiated and addressed aggression toward males during 23 events, with males responding three times with counter-aggression. Since only females initiated and addressed aggression toward males, females were considered to be dominant over males, at least in the feeding context.

Three groups of crowned sifakas (***P. coronatus)*** were observed for 273 h in the Antrema Forest Station in north-west Madagascar. Out of 39 agonistic interactions, female initiated 80% agonistic interactions toward males, but could only dominate 50% of males (Ramanamisata et al., 2014).

In diademed sifakas (***P. diadema)*** three groups were observed for 325 h outside the reproductive season at Tsinjoarivo. In total, 21 agonistic interactions were observed, of which 11 occurred between the sexes and 10 between males. Females won 88% of conflicts with males and dominated 83% of males (Rasolonjatovo and Irwin, 2020).

In Milne Edwards sifakas (***P. edwardsi***), data on intersexual relationships were obtained from observations of four groups over a period of 15 years at Ranomafana National Park. Each focal animal was observed for about 7.9 ± 2.9 h. Milne Edwards sifakas exhibited an aggression rate of 0.22 interactions/h. Out of 1,426 agonistic interactions 1,410 were decided (98.9%). 825 agonistic interactions occurred between the sexes and females won 94% of all conflicts with males, but information on the number of males dominated by males was not provided (Pochron et al., 2003).

Four adult wild-caught golden-crowned sifakas (***P. tattersalli)*** were observed for 4,110 h at the Duke Lemur Center. Females won 90% of conflicts over males and could dominate all males (Wallace et al., 2016).

Ten groups of Verreaux's sifakas (***P. verreauxi)*** were observed throughout the year for 2,808 h at Kirindy Forest. A total of 383 agonistic interactions, of which 345 were decided (90.1%) and 38 undecided, were observed in a feeding context. Females won 91% of intersexual conflicts and could dominate 83% of

males (Kappeler et al., 2009). In another study, four groups of Verreaux's sifakas were observed for 4,965 h over a period of 9 years in Kirindy Mitea National Park (Voyt et al., 2019). A total of 483 decided agonistic interactions were observed. In 342 agonistic interactions, the age of the two conflicting partners was known. Young females of 3 years won only 30% of conflicts with males, females between an age of four to six won on average more than 50% of intersexual conflicts, whereas adult females older than 7 years won 100% of their conflicts with males. These data suggest that female dominance becomes more unambiguous with female reproductive maturity.

Although sifaka males are occasionally able to win individual conflicts over females, females win the majority of fights and are able to dominate most males in their groups. Hence, sifakas can be clearly classified as exhibiting widespread female dominance. Overall, all species of the indriids which have been studied so far, exhibit female dominance.

Lemurs (Lemuridae)

The family of lemurs contains 21 species in 5 genera, of which information on intersexual dominance relations exists for 14 species from mostly observational studies in captivity and the wild.

Prolemur

The social behavior of greater bamboo lemurs, ***Prolemur simus***, has not been systematically studied. In the wild, they live in groups with multiple adult males and females (Frasier et al., 2015). In captive colonies in France, however, unsystematic behavioral observations revealed that two adult males cannot be kept together. The same is true for unrelated adult females and related females with offspring. According to Roullet (2011), males can become aggressive toward keepers and also dominate females. If confirmed by specific behavioral studies, *P. simus* would be the only known lemur species with exclusive male dominance.

Hapalemur

Information on intersexual dominance relations in pair-living bamboo lemurs is available from three out of five species. In ***Hapalemur alaotrensis***, four wild groups were observed for 4 months outside the reproductive season (Waeber and Hemelrijk, 2003). All but one intersexual agonistic interaction were decided, and the vast majority of them was over access to food. Of 260 male–female conflicts, 77% involved only submissive behavior, and in 83% of those only males exhibited submission. Nonetheless, in some conflicts females submitted to males, but it remains unknown how many different females exhibited submission, whether this included some of the juvenile females included in the study, and whether females that exhibited submission in a conflict with a male were able to elicit submission from the same male in other conflicts. Despite this lack of detail, it appears fair to conclude, based on the presently available data, that female Alaotran bamboo lemurs exhibit female dominance in the vast majority of agonistic interactions with adult males.

A total of 428 agonistic interactions were observed in two small groups and one pair of wild southern bamboo lemurs, ***H. meridionalis***, during 1,762 h distributed across a full year (Eppley et al., 2017). Females initiated and won more than 90% of these conflicts (79.8% over access to food) and were twice as likely to target a male than males that initiated agonistic interactions. All three study units contained one adult male and two or one adult females, and a female took the dominant position in all three units.

In three groups of wild gray bamboo lemurs, ***H. griseus***, observed over 3 months outside the reproductive season, only seven agonistic interactions between males and females were recorded in 337 h of focal animal observations, and in 3 (42.9%) of them, females directed aggression toward males (Foreit, 2016), but submissive behavior was not recorded in this study. Thus, sex did not predict the direction of aggression, but the number of observed conflicts is very low. A behavioral study of five captive pairs or small family groups lasting over a year yielded details on 42 intersexual agonistic interactions, of which the females decided 81% in their favor (Digby and Stevens, 2007). Thus, rates of agonistic interactions in these specialized folivores are low, and females win most, but by far not all agonistic interactions with adult males.

Lemur

Ringtailed lemurs, ***Lemur catta***, were the first lemur species for which female dominance was reported (Jolly, 1966b). They form the largest groups of all lemurs with multiple adult males and females. Numerous studies of wild and captive populations have since confirmed that all adult females unconditionally dominate all adult males. We therefore refer to only one captive and two different wild studies with large sample sizes.

Studying two semi-free ranging captive groups at the Duke Lemur Center, Pereira and Kappeler (1997) observed 495 agonistic interactions between males and females in more than a year of observations, and 99.5% of them were decided in favor of females. Most interactions consisted of spontaneous male submission whenever males and females came into close proximity. In a study of two wild groups at Beza Mahafaly, Sauther (1993) recorded 2,301 agonistic interactions during 1,800 h of observations, with 86% of them occurring over food resources. In 35 of intersexual agonistic interactions, a male displaced a female, but the latter were all young and nulliparous. In contrast, females won 96.9% of their agonistic interactions with males, and the rates of their conflicts peaked during the late lactation period. A 4-month study of two groups at Berenty Reserve during the birth season confirmed the pattern of unambiguous female dominance (Nakamichi and Koyama, 1997). Females were winners and males were losers in all of the 709 decided agonistic interactions between females and males, and females were dominant over males in 90 of 91 possible female–male dyads in these two groups; the remaining dyad was never observed to interact. Thus, ringtailed lemurs exhibit ubiquitous female dominance under variable environmental conditions in all behavioral contexts.

Varecia

One field study focused on intersexual dominance relations in black and white ruffed lemurs, ***Varecia variegata***.

Overdorff et al. (2005) observed two groups for more 17 months, but they were not able to consistently decide which animals were winners and losers. Moreover, one group was socially instable for most of the study period. In a stable group of two females and two males, one female dominated all other group members, but submissive signals were rarely exchanged, and 45 of 49 submissive signals were given by one male toward the dominant female. In a year-long study of a captive pair living in a natural habitat enclosure at the Duke Lemur Center with their three offspring, 76.5% of 47 agonistic interactions between all group members were decided, and 97.1% of the decided interactions were won by females (Raps and White, 1995). Only 25.7% of females' 35 wins lacked female aggression, however; i.e., spontaneous male submission is not common. A 2-month study of a semi-free ranging pair and their 5 offspring at Duke Lemur Center recorded 46 agonistic interactions, of which all but one (97.8%) were won by females (Kaufman, 1991).

Two captive groups of red ruffed lemurs, ***V. rubra***, consisting of a breeding pair and their offspring, were studied at the Duke Lemur Center between September and April (i.e. including the mating and birth season; Raps and White, 1995). All 348 agonistic interactions were decided, 96.5% of them were won by females, and 69.5% of those involved female aggression. A 20 h study of a captive group of three females and two males reported 25 agonistic interactions, of which 96% were decided; all of them in favor of females (Meyer et al., 1999).

Thus, despite a lack of longer studies of multiple groups, the available evidence indicates that ruffed lemur females are generally able to dominate males and that female aggression appears to be often required to elicit male submission.

Eulemur

Of the 12 species of true lemurs, data on intersexual dominance relations are available for seven of them; most of them from studies in captivity. Between September and May (i.e. including the mating and birth season), four groups of crowned lemurs, ***Eulemur coronatus***, were studied at Mulhouse Zoo (Marolf et al., 2007). A total of 83% of 424 intersexual agonistic interactions were decided, and females won 81% of them. Females were able to elicit much more submissive behavior from males than *vice versa*, but in one of the groups, the only male dominated the only adult female. The intersexual agonistic interaction rate increased during the breeding season in only one group. In a captive group at the Duke Lemur Center studied across a year, females won 97% of all decided agonistic interactions (N = 105) with males (Pereira et al., 1990).

In two family groups of redbellied lemurs, ***E. rubriventer***, at Mulhouse Zoo, 53.1% of 64 agonistic intersexual conflicts were decided, and females won 88.2% of those (Marolf et al., 2007). Females never showed spontaneous submission toward males. In one of the groups, most conflicts occurred during the breeding season. The majority of intersexual agonistic conflicts in a year-long study of two wild family groups at Ranomafana National Park occurred in the context of infant transfer, when the mother cuffed the male in the process of transferring an infant on his back for carrying (Overdorff and Tecot, 2006).

Seven groups of blue-eyed black lemurs, ***E. flavifrons***, were studied at the Duke Lemur Center for 260 h in June and July (i.e., during the non-reproductive season; Digby and Kahlenberg, 2002). Of 293 agonistic interactions between males and females, females won 99% of them. Males elicited submissive behavior from a female on only four occasions. Only 19% of agonistic interactions involved spontaneous male submission. In a subsequent study of the same population, females won 98.6% of 506 intersexual agonistic interactions, and 65.7% of 589 dominance interactions initiated by females involved aggression on their part (Digby and Stevens, 2007).

In one captive group of black lemurs, ***E. macaco***, studied for 2 months after the mating season at the Strasbourg Primate Center, 46% of 81 intersexual conflicts were decided and the majority (95.6%) of decided conflicts were won by the aggressor independent of its sex (Roeder et al., 2002). In an experimental dominance study with black lemurs, females were dominant over males in a competitive drinking test, but no details on the nature of their conflicts are available (Fornasieri et al., 1993).

Two groups of brown lemurs, ***E. fulvus***, were studied at the Strasbourg Primate Center for 233 h outside the mating season (Roeder et al., 2002). Of 102 intersexual conflicts, only 27.7% were decided and in 92.4% of the decided conflicts, the initiator prevailed, independent of sex. Similarly, in an experimental dominance study with brown lemurs, sex had no effect on the outcome of conflicts in a competitive drinking test (Roeder and Fornasieri, 1995).

In two groups of redfronted lemurs, ***E. rufifrons***, studied in natural habitat enclosures at Duke Lemur Center, only 33.5% of 474 conflicts were decided, and less than 33% of those were decided in favor of females (Pereira and Kappeler, 1997). Similar results were obtained in an independent study of the same captive population (Pereira et al., 1990), with only 31% of agonistic interactions being decided. In a wild group at Ranomafana National Park, this percentage was at 61% (N = 279), and females won only 13% of the 172 decided agonistic interactions with males (Pereira et al., 1990). Thirty-four percent of conflicts at Ranomafana included female submission toward males and 65% male aggression toward females. A field study of two groups at Kirindy Forest between April and August (i.e. including the mating season) revealed that male-male agonistic interactions were most frequent and that more than 80% (N = 258) of them were decided (Ostner and Kappeler, 1999). Intersexual interactions were much rarer and only 27% of them were decided. Only one conflict between females was observed in 1,023 observation hours. Based on decided agonistic interactions, one male appeared on top of the dominance hierarchy of both groups.

Finally, in two wild family groups of mongoose lemurs, ***E. mongoz***, females were reported to have priority of access to food in all conflicts with males, but no details on the number or nature of conflicts was provided (Curtis and Zaramody, 1999).

Thus, intersexual dominance relations among true lemurs are highly variable. Females are dominant in some species, but sex has no effect on the outcome of agonistic interactions in others. Aggression appears to be required to win agonistic interactions and exclusive submissive behavior is rare. Feeding and reproduction are contexts in which conflict rates are high,

but most studies suffer from either short duration, few conflicts or a lack of relevant detail.

The available quantitative data offer very few opportunities for explorative statistical analyses. To assess potential impacts of study type (observation vs. experiment), setting (captivity vs. wild) or season (mating season included or not), not enough studies of the same species under different conditions are available. One strong prediction is that the ability to win agonistic interactions with members of the opposite sex is based on physical superiority. However, average sexual size dimorphism among lemurs is close to 1 with a mean ± SD of 0.97 ± 0.09, a minimum of 0.82 and a maximum of 1.19 (**Table 1**). Sexual size dimorphism is nonetheless negatively correlated with the average proportion of conflicts won by females (**Figure 1**; Pearson, N = 36 species, r = –0.38, p = 0.022), but only if *Prolemur simus* is included (with a value of 0% female wins; Roullet, 2011). After excluding *P. simus*, this correlation is no longer significant (**Figure 1**; Pearson, N = 35 species, r = –0.25, p = 0.149), however. Hence, quantitative data from *Prolemur,* but also additional species, on intersexual dominance are required to determine whether sexual size dimorphism covaries indeed with the proportion of conflicts females win over males.

APPRAISAL OF THE EVIDENCE

In striking contrast to most other primates and mammals, the ability of adult females to consistently dominate adult males is clearly widespread among the primates of Madagascar. However, there is more variation in intersexual dominance relations among and within species than previously acknowledged, ranging from well-documented empirical support for invariable female dominance in some species to possible male dominance in others. Given the nature of the available evidence, however, only a broad qualitative assessment of the dimensions and causes of this variation is currently possible.

First, females in all five families and all the genera studied so far are able to evoke submissive behavior from adult males. *Prolemur* may be an exception, but only systematic quantitative data will allow a firm assessment of this species in the future. Given this taxonomic distribution of female dominance, a phylogenetic reconstruction conducted for purely illustrative purposes (**Figure 2**) revealed that this ability has already characterized ancestral lemurs – perhaps even the first colonizers – than to postulate multiple evolutionary origins of female dominance (see also Petty and Drea, 2015; Lewis, 2018). The issue of whether the absence of male dominance and male-biased sexual size dimorphism in lemurs is just an idiosyncrasy of that lineage, or whether the colonization or ecology of Madagascar have prompted adaptations that are only rarely found in other mammals remains difficult to resolve, but some comparative evidence suggests that a combination of these factors might be implicated (Kappeler et al., 2019).

Second, substantial variation in the nature of intersexual dominance among closely-related species within the same genus indicates that environmental and/or social factors have shaped the variation in social structure seen among contemporary lemur species. The standardized experiments with *Microcebus*, but also the various observational studies of *Eulemur* and *Propithecus* revealed intriguing variation that is not obviously linked to a particular habitat, season or reproductive phase. Observations of wild species have emphasized feeding competition as a frequent context in which females dominate males, but captive and experimental studies have indicated that intersexual agonistic interactions are neither limited to this situation nor particular to any species. The phylogenetic reconstruction also indicates that the average proportion of intersexual conflicts won by females has been reduced independently in some taxa in all families, except for the Daubentoniidae (**Figure 1**), suggesting that intersexual dominance relations continue to evolve in response to selective factors that remain obscure for the time being.

The same applies to contexts related to reproduction. Female rejections of unwanted male advances and defense of vulnerable infants provide contexts in which male and female interests collide, and where females have greater power because they control the resource males want (fertilizable eggs), but the studies included in this review did not reveal a systematic increase in female dominance during the mating season. Furthermore, the available studies do not report data for the mating season and non-mating season separately, precluding formal statistical comparisons. We could only document a possible trend for a reduction in the proportion of conflicts won by females with an increasing size advantage of males, suggesting that physical superiority is involved in determining intersexual dominance relations. Using a different measure of female dominance, Hemelrijk et al. (2008) found no correlation with sexual size dimorphism across 22 primate species. Also, in spotted hyenas female dominance is independent of body mass (Vullioud et al., 2019). Ideally, however, year-round studies of multiple groups, pairs or large samples of known individuals should be conducted to record variation in the frequency, nature and contexts of agonistic interactions between opposite- and same-sex opponents to have a quantitative basis for more systematic comparisons in the future.

Finally, and related to this last point, the level of detail with which different studies have reported their results is highly heterogeneous, also hampering comparative analyses aimed at understanding the levels and sources of variation in intersexual dominance relations. Whereas many studies of dominance in lemurs have reported more details about the actual interactions than studies of other primates and mammals – especially with respect to the occurrence of submissive behavior - our review revealed that there is no generally agreed-upon standard for reporting data on agonistic interactions. For example, it would be desirable – in our view – to report for each sex combination of dyads the rate of conflicts, the proportion of decided and undecided conflicts, the proportion of conflicts with submissive signals and the social context of interactions. Interactions with juveniles should be reported separately because size differences may distort intersexual dominance relations. Moreover, at the level of summarizing and analyzing these data for group-living species, it should be reported whether and how these interactions were used to generate a hierarchy, as well as their basic properties like linearity and transitivity (see Levy et al., 2020). From

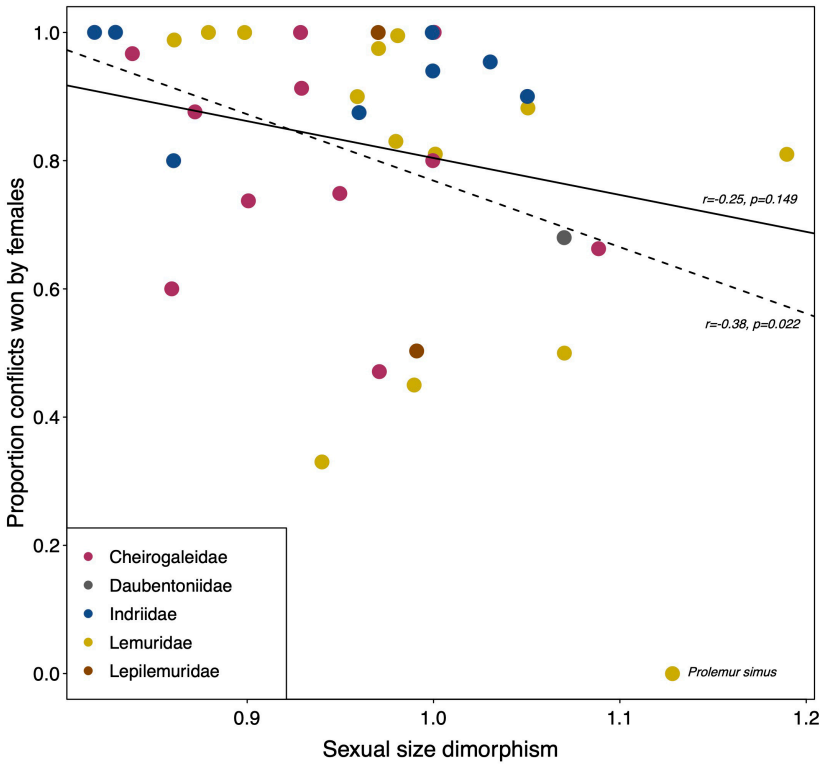

FIGURE 1 | Relationships between the average sexual size dimorphism in body mass and the average proportion of conflicts females won over males across the members of different lemur families. Dashed line indicates the Pearson correlation including *Prolemur simus*; solid line presents the correlation excluding *P. simus*. All data from **Table 1**.

dominance hierarchies, it is also possible to determine the number or proportion of members of the opposite sex dominated by any female or male to calculate a corresponding summary statistic (see e.g., Kappeler, 2022). Finally, whereas social network analyses may provide additional insights about the structure of intersexual dominance relations, the groups of most lemur species were too small to apply these methods in meaningful ways (see e.g., Eppley et al., 2017), but new methods for small groups are now available (Coelho et al., 2020).

THE EVOLUTION OF FEMALE DOMINANCE

As always, a Tinbergian perspective is most helpful for illuminating the evolution of a social phenomenon like intersexual dominance (Bergman and Beehner, 2021; Smith et al., 2021). First, the ability of female lemurs to evoke submission from adult males *per se* is proximately not dependent on physical superiority, but might be modulated by relatively small variation in sexual size dimorphism, and it is also not restricted to any particular social context like feeding or reproduction (see also Kappeler, 1990b). The relative roles of female aggression and male submission in generating decided agonistic interactions in different species remains unresolved, however, until more studies report details on the proportion of conflicts with (spontaneous) male submission. In particular, it would be of interest to have a more comprehensive understanding of the distribution of submissive signals as well as their importance in intersexual, but also same-sex interactions (Reddon et al., 2021). Focusing on the proximate control of female aggression and masculinization in lemurs, several studies have explored the possible role of androgenic steroid hormones in shaping female aggressive phenotypes (Petty and Drea, 2015). Whereas lemur females are strikingly masculinized in their genital morphology, this line of research has not suggested a uniform ultimate reason why female dominance might be adaptive.

Second, an ontogenetic perspective suggests that the ability of females to win agonistic interactions with males emerges in close temporal proximity with sexual maturity because young females in ringtailed lemurs (Pereira, 1993), Verreaux's sifakas (Voyt et al., 2019) and gray mouse lemurs (Hohenbrink et al., 2015a,b) begin eliciting male submission at that developmental stage. Because these species represent different families, this functional relationship between female dominance and female reproduction is presumably ancestral for lemurs, but additional studies on the ontogeny of female dominance would be welcome.

Third, compared to other mammals, where unanimous dyadic female dominance is limited to spotted hyenas and less comprehensive forms of female dominance to a handful of other species (Kappeler, 1993; Koren et al., 2006; Watts and Holekamp, 2007; Dunham, 2008; Koren and Geffen, 2009; French et al., 2013;

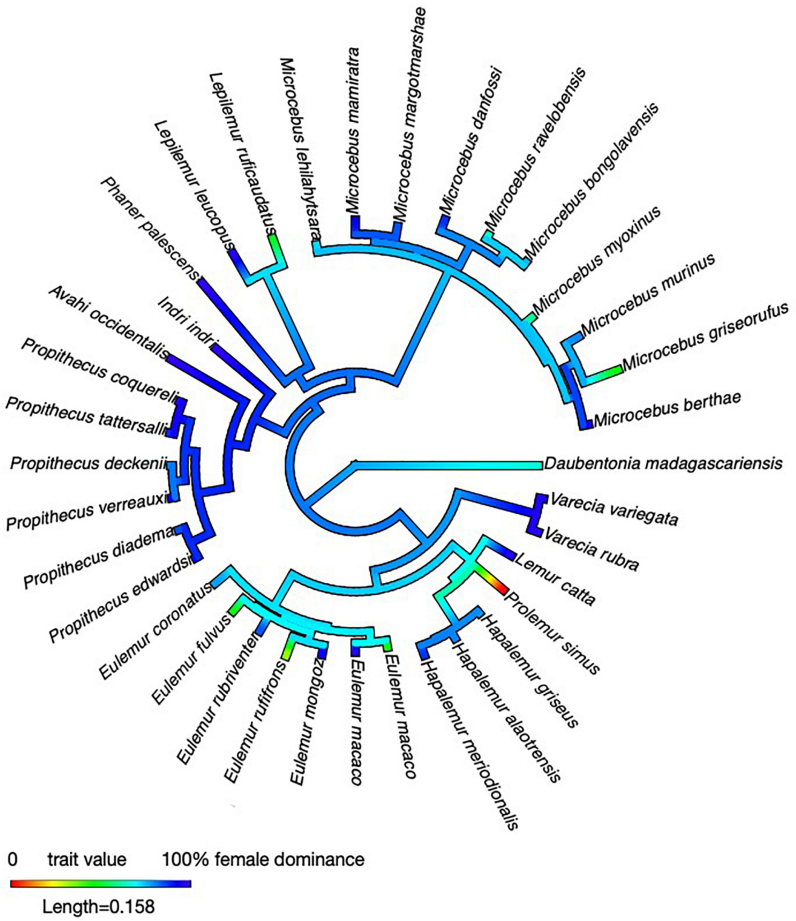

FIGURE 2 | Phylogenetic reconstruction of intersexual dominance across the Lemuriformes. We conducted an ancestral state reconstruction using the package "phytools" (Revell, 2012) in R (version 4.0.3; R Core Team, 2020). For illustrative purposes, we mapped female dominance, i.e., the percentage of conflicts won by females, on a consensus tree obtained from the 10k trees website (Arnold et al., 2010). Female dominance varies between 0 and 100%, making a formal reconstruction formally challenging, also because no obvious criteria for a discrete classification (female dominance: "yes" or "no" exist). All data were taken from **Table 1**.

Surbeck and Hohmann, 2013; Kappeler and Fichtel, 2015; Holekamp and Sawdy, 2019; Vullioud et al., 2019), lemurs represent an unusual taxon from a phylogenetic perspective. This concentration of species with female dominance has engendered evolutionary explanations that focus on idiosyncrasies of either lemurs or Madagascar, or both. In some cases, these hypotheses have incorporated functional aspects that offer an ultimate explanation.

The predominant explanation for the prevalence of female dominance among lemurs is based on a combination of phylogenetic and functional considerations. It postulates that lemur females face higher energetic costs of reproduction in combination with food scarcity than other primates, so that they benefit from priority of access to contested food resources during energetic bottlenecks ('energy conservation hypothesis': Jolly, 1984; Wright, 1999), and males are selected to defer to them because they avoid the costs of escalated fighting by doing so ('cost-asymmetry hypothesis', Dunham, 2008). Empirical tests of the assumptions and predictions of this hypothesis have focused on lemur life histories (Young et al., 1990; Meyers and Wright, 1993; Kappeler, 1996) and Madagascar's climate and phenology (Dewar and Richard, 2007), but have not produced unanimous support (Federman et al., 2017). In addition, it does neither explain the absence of male-biased sexual size dimorphism and dominance nor the even adult sex ratios of group-living lemurs. For a more conclusive evaluation of this group of hypotheses, future research should generate data sets that combine details of male–female interactions, developmental and reproductive schedules as well as climatic and phenological variables from a broad range of species, ideally including sets of sympatric species.

The 'evolutionary disequilibrium hypothesis' explained female dominance and a complex of functionally related traits as the result of largely non-adaptive consequences of human-induced environmental changes in the last few millennia, creating an evolutionary disequilibrium between current ecological conditions and lemur traits. It posited that female dominance is part of a complex of traits of diurnal group-living lemurs that persisted after very recent evolutionary transitions

from nocturnal, pair-living ancestors following the Holocene extinction of large predatory eagles and large-bodied subfossil lemurs (van Schaik and Kappeler, 1996). Because the absence of sexual size dimorphism and consistent male dominance also characterize many pair-living mammals, their prevalence among group-living lemurs does not represent an adaptation to current ecological conditions but rather an example of phylogenetic inertia because a few centuries have not provided enough time for adaptations to the new ecological niche. This hypothesis has provoked several studies challenging its core assumption (e.g., Kirk, 2006), and it does not explain the prevalence of female dominance among the solitary lemur species. It is not incompatible with the energy conservation hypotheses, however, and also highlights links between lemur ecology and behavior.

The most recent attempt to take into account and reconcile the existing hypotheses about underlying adaptive function and proximate causation added a potential developmental mechanism linking maternal stress and filial masculinization to outline an evolutionary scenario for its canalization (Kappeler and Fichtel, 2015). Accordingly, lemur females are assumed to be subject to significant and unique patterns of resource limitation, especially during reproduction, creating recurrent energetic limitations. Lemur females, and in particular those of larger species with gestation and lactation periods spanning several months, are therefore potentially exposed to massive environmental stress during many, if not most, of their lifetime reproductive events because the exact timing of food availability is poorly predictable. The resulting physiological stress response would be exacerbated by feeding competition and leads to the masculinization of daughters which ought to be better prepared to compete with other females in adverse environments. Thus, natural selection will enhance the effects of maternal programming and synergistic epistasis, resulting in canalization in competitive traits that also allow female dominance as a by-product over evolutionary times, but the generality of the proposed underlying processes awaits additional empirical study.

The behavioral studies summarized in this review have not contributed new insights about the ecological and physiological factors implicated in shaping the evolution of female dominance. Yet, the confirmation that it has evolved in representatives of all 5 extant families indicates that it has either characterized the first lemurs colonizing Madagascar or that it has evolved very soon after the colonization. Given that female dominance is not known to occur in the lineage representing the last shared common ancestors on the African mainland (Bearder, 1999), it seems most parsimonious to assume that it evolved soon after the colonization under unique ecological conditions characterizing the various Malagasy forest habitats. The interspecific variation in the extent of female dominance highlighted here suggests, however, that intersexual dominance relations are subject to adaptations to variable social and ecological factors.

CONCLUSION

The ability of adult females to consistently dominate adult males is widespread among the primates of Madagascar, suggesting that it has evolved soon after the colonization of the island by lemurs. There is much more interspecific variation in intersexual dominance relationships than previously acknowledged, however, and variation even exists within some species. Female dominance is typically achieved *via* male submission, and male aggression toward females is relatively rare. Female lemurs do not consistently enjoy physical superiority over males, and other proximate bases of their power remain unknown. Female dominance emerges ontogenetically along with female sexual maturity, suggesting some functional link to sex-specific reproductive strategies, but it is not limited to the context of mating where females have greater power. Lemur- and Madagascar-specific explanations for the evolution of female dominance have emphasized links between ecology and behavior and the energetics of reproduction, but a lack of comparative data, also from other Malagasy and Southern African mammals, has hampered progress with testing assumptions and predictions of existing hypotheses.

AUTHOR CONTRIBUTIONS

PK drafted the manuscript to which CF and UR made substantial contributions. All authors contributed to the article and approved the submitted version.

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Sex and dominance: How to assess and interpret intersexual dominance relationships in mammalian societies

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The causes and consequences of being in a particular dominance position have been illuminated in various animal species, and new methods to assess dominance relationships and to describe the structure of dominance hierarchies have been developed in recent years. Most research has focused on same-sex relationships, however, so that intersexual dominance relationships and hierarchies including both sexes have remained much less studied. In particular, different methods continue to be employed to rank males and females along a dominance hierarchy, and sex biases in dominance are still widely regarded as simple byproducts of sexual size dimorphism. However, males and females regularly compete over similar resources when living in the same group, and sexual conflict takes a variety of forms across

societies. These processes affect the fitness of both sexes, and are mitigated by intersexual hierarchies. In this study, we draw on data from free-ranging populations of nine species of mammals that vary in the degree to which members of one sex dominate members of the other sex to explore the consequences of using different criteria and procedures for describing intra- and intersexual dominance relationships in these societies. Our analyses confirmed a continuum in patterns of intersexual dominance, from strictly male-dominated species to strictly female-dominated species. All indices of the degree of female dominance were well correlated with each other. The rank order among same-sex individuals was highly correlated between the intra- and intersexual hierarchies, and such correlation was not affected by the degree of female dominance. The relative prevalence of aggression and submission was sensitive to variation in the degree of female dominance across species, with more submissive signals and fewer aggressive acts being used in societies where female dominance prevails. Thus, this study provides important insights and key methodological tools to study intersexual dominance relationships in mammals.

KEYWORDS

dominance, sex, hierarchy, mammals, methodology

Introduction

When the Norwegian zoologist Schjelderup-Ebbe (1922) published his dissertation on the social psychology of chickens a century ago, he was the first to report that the directionality and consistency with which hen peck at each other during feeding and resting yields a stable arrangement among individuals that he called a pecking order. As in other species, dominance relationships among chicken are established and maintained through agonistic interactions whereby one individual may exhibit aggressive behavior, whereas the partner either displays submissive behavior or avoids confrontation with the aggressor altogether (Rowell, 1974). Other, structurally more complex types of hierarchies have since been described for various animal societies in which individuals recognize individual conspecifics and remember the outcome of previous agonistic interactions with co-residents (Reddon et al., 2021). Whereas solitary or unfamiliar animals can also establish a dominance relationship without prior interaction, for example, based on mutual assessment of body size, ornaments or other intrinsic cues of fighting ability, we are here primarily interested in this aspect of the social structure of species that live permanently in groups that contain both sexes because social dominance represents a prominent feature of many animal societies.

Dominance relationships have various determinants that are not mutually exclusive and can feed back upon each other in determining the outcome of an agonistic interaction (Dehnen et al., 2022). First, in some species, a given dyadic dominance relationship reflects differential social support received by each member of the dyad (Clutton-Brock and Huchard, 2013a,b), either in the form of parental (Holekamp and Smale, 1991) or non-parental support (Schülke et al., 2010). Second, memories of previous interactions with known individuals can promote a learning effect that leads individuals to exhibit submissive behavior toward certain other conspecifics (Guhl, 1968). The effect of this dyadic interaction-outcome history is further reinforced by the winner-loser effect (Chase et al., 1994), according to which winning increases the probability to be victorious again and losing makes it more likely that the victim loses again in the next fight against any other opponent (Rutte et al., 2006; Franz et al., 2015). Finally, dominance relationships are often based upon an asymmetry in agonistic power grounded on intrinsic attributes, such as physical superiority, fighting ability, motivation, or leverage that are often age-based (Hand, 1986; Lewis, 2002; Jonart et al., 2007; Dunham, 2008; Clutton-Brock and Huchard, 2013a,b; Dehnen et al., 2022; Tibbetts et al., 2022). In species with pronounced sexual size dimorphism and/or elaborate weapons, these intrinsic attributes are linked to sex, with members of the larger and/or better armed sex often using their attributes to establish and stabilize dominance relationships with members of the opposite sex (Kappeler, 1993; Lewis, 2018), just as size and strength are important determinants of within-sex dominance. However, recent evidence highlighted that sex differences in physical attributes may often fail to predict who is dominant

in an intersexual relationship, as in bonobos (*Pan paniscus*) and spotted hyenas (*Crocuta crocuta*) (Surbeck and Hohmann, 2013; Vullioud et al., 2019).

In species in which groups consist of permanently associated males and females, past research has often focused on intrasexual dominance relations because they are thought to mediate access to fitness-limiting factors, such as mates and resources. As a result, most previous studies of dominance hierarchies have been framed in separate theoretical frameworks. Studies of female dominance relations focused on the ecological drivers of interspecific variation (Sterck et al., 1997; Clutton-Brock and Janson, 2012). Studies of male dominance relationships, in contrast, focused on their functional outcomes for mating access and reproductive skew (Cowlishaw and Dunbar, 1991; Alberts, 2012). However, such a binary approach overlooks the potential importance of intersexual agonism for the fitness of both sexes. First, when males and females live in the same group, competition can occur both within and between the sexes for access to various resources, including – but not necessarily limited to – the feeding context (Valé et al., 2020; Koenig et al., 2022). Second, sexual conflict is nearly ubiquitous, and takes various forms that all generate intersexual strife (Chapman et al., 2003; Davidian et al., 2022), which affects the fitness of both sexes and may be mitigated by intersexual hierarchies. Thus, while it may make sense to use separate intrasexual hierarchies for species with pronounced sexual size dimorphism, with sex differences in the steepness, linearity and stability of the within-sex hierarchies, and in which the mechanisms of rank acquisition differ between the sexes, this approach may not be appropriate for other species.

A few studies indicate that sex is one key variable for scrutinizing dominance hierarchies in more detail. First, in some species individuals are distributed within a group's hierarchy as a function of their sex, with either all or most males outranking all females or – more rarely – *vice versa* (Kappeler, 1993; Smuts and Smuts, 1993; Stevens et al., 2007; Surbeck and Hohmann, 2013; Izar et al., 2021). Such sex clusters likely reflect sex differences in morphology, physiology or life-history that underlie agonistic power and therefore offer an opportunity to identify sex-specific determinants of dominance. Second, males and females compete for different resources, and may therefore employ different strategies to establish and maintain their dominance rank among their same-sex peers, with unknown consequences for the establishment of intersexual hierarchies. Notably, the steepness, linearity and stability of the male and female hierarchies often differ. In chimpanzees and gorillas, for example, males have conspicuous and relatively despotic dominance hierarchies, whereas dominance relations among females are more elusive and are based on age-based queuing conventions (Stevens et al., 2007; Foerster et al., 2016). In Barbary macaques, the opposite pattern has been found, with males being more egalitarian and females more despotic in dominance style (Preuschoft et al., 1998; Hemelrijk and Gygax, 2004). Contrasting hierarchies across dyads of same- and opposite-sex members can therefore reveal informative subtleties on sex differences in social competition beyond species differences. Finally, the mechanisms of rank acquisition may differ between the sexes, with males typically relying on intrinsic attributes to compete for high rank, whereas female ranks tend to depend more often on social support (Holekamp and Smale, 1991; Clutton-Brock and Huchard, 2013b).

Nonetheless, dominance relationships between the sexes have not received the same theoretical and empirical attention as same-sex dominance relationships. Because male-biased sexual dimorphism is widespread among mammals (Lindenfors et al., 2007) and represents a default expectation based on conventional sex roles, the ability of males of these species to dominate females was typically considered an unavoidable side-effect of physical superiority and greater aggressiveness, rather than as an adaptive trait *per se* (Kappeler, 1993; Smuts and Smuts, 1993; Lewis, 2018). In contrast, the rare cases of female dominance often required special explanation and generated several hypotheses that typically invoke taxon-specific factors to explain the evolution of this sex role "reversal" (Jolly, 1984; Richard and Dewar, 1991; van Schaik and Kappeler, 1996; Wright, 1999; Dunham, 2008; Kappeler and Fichtel, 2015). These few taxa or studies were not deemed of enough general interest, however, to prompt a general synthesis of intersexual relationships.

The dichotomous classification of species as either male- or female-dominated has been challenged by more recent studies indicating that these patterns only represent the endpoints of a continuum (Hemelrijk et al., 2008, 2020; Davidian et al., 2022; Kappeler et al., 2022). It is now more widely appreciated that there are taxa where members of one sex only win a proportion of all agonistic interactions with the members of the other sex or where they dominate only some, but not all, opposite-sex individuals (Surbeck and Hohmann, 2013; Young et al., 2017, Vullioud et al., 2019; Hemelrijk et al., 2020). In addition, different methods continue to be employed to rank males and females along a dominance hierarchy (Pereira and Kappeler, 1997; Hemelrijk et al., 2008), potentially obscuring interesting biological patterns. In order to analyze this variation in a comparative fashion, comparable data on intersexual dominance relationships are required. However, existing studies have used various methods for recording details of agonistic interactions, for inferring dominance relationships, and for determining dominance hierarchies, and different species use different types and variable proportions of acts and signals to establish dominance relationships, thereby hampering comparative studies on this topic. We are therefore only beginning to explore whether different methods to analyze agonistic interactions are equivalent or whether some methods should be preferred or discouraged (Sánchez-Tójar et al., 2018; Vilette et al., 2020).

The general aim of this study is, therefore, to systematically determine the consequences of using different behavioral data,

criteria and methods for inferring patterns of intersexual dominance relationships. Specifically, we aim to make recommendations about standardized methods of data collection and analyses for future studies of intersexual dominance relationships that go beyond taxon-specific idiosyncrasies. We are also interested in possible similarities across species in the nature and pattern of intersexual dominance relationships. For instance, it remains unknown whether an individual's position in the intrasexual hierarchy relates to its position in the intersexual hierarchy and, hence, whether intersexual dominance patterns are an emergent property of intrasexual ones.

To this end, we have collated datasets from nine mammalian species which were chosen because they differ in the degree to which members of one sex dominate the members of the other sex, ranging from complete male dominance to complete female dominance. Our aim was to explore the consequences of using different criteria and procedures for describing intra- and intersexual dominance relations in this sample of animal societies and not a comparative study across a wide range of taxa and social systems. Most of these datasets are based on observations spanning at least a full year for at least two different groups, thereby accounting for seasonal variation and group idiosyncrasies. With this dataset, we (1) calculated and compared different indices of the degree of intersexual dominance in a group, (2) examined whether an individual's rank in the same-sex hierarchy predicts its position in the intersexual hierarchy, i.e., whether high-ranking females in the female hierarchy are more likely to dominate males, for example, and if the degree of correlation between intra- and intersexual hierarchy changes along the intersexual dominance spectrum, and (3) explored whether within- and between-sex conflicts differ in nature and intensity in terms of their reliance on aggressive and submissive behavior along the intersexual dominance spectrum. Taken together, our study provides a first set of recommendations and predictions for future studies aimed at explaining interspecific variation in intersexual dominance.

Materials and methods

Study species and data collection

Data on agonistic interactions were collected from nine different mammalian species: spotted hyenas (*Crocuta crocuta*), rock hyraxes (*Procavia capensis*) and seven primates including two lemurs: Verreaux's sifakas (*Propithecus verreauxi*) and redfronted lemurs (*Eulemur rufifrons*), four Old World monkeys: chacma baboons (*Papio ursinus*), crested macaques (*Macaca nigra*), mandrills (*Mandrillus sphinx*), and vervet monkeys (*Chlorocebus pygerythrus*) and one ape: bonobos (*Pan paniscus*), as part of nine long-term individual-based field studies, including the Ngorongoro Hyena Project, Ein Gedi Rock Hyrax Sociality Project, Kirindy Forest Lemur Project, Tsaobis Baboon Project, Macaca Nigra Project, Mandrillus Project, Inkawu Vervet Project and the Kokolopori Bonobo Research Project. All studies were approved and authorized by the respective national authorities. The localization and ecology of each field site, as well as the demographic, life-history and behavioral monitoring of each study population are described in the **Supplementary Materials**, alongside the species-specific agonistic behavioral repertoire.

Data on agonistic interactions were recorded as detailed in the **Supplementary Materials** and grouped by year for each species and study group, yielding 24 group-years of data (range 1–4 per species). An agonistic interaction was defined by the expression of at least one species-specific agonistic behavior (see Hausfater, 1975). Following Deag (1977), agonistic behavioral elements were functionally characterized as either aggressive or submissive (see also Walters, 1980). Structurally, we distinguished between acts, which involve physical contact or locomotion, such as lunging or fleeing, and visual or vocal signals, such as non-physical threats or grimacing (see Pereira and Kappeler, 1997). We considered only dyadic interactions between adult individuals.

Group size ranged between 4 and 72 adult individuals, including 1–62 females and 2–26 males (**Table 1**). For each dataset, the corresponding co-author(s) entered the data into a standardized template. In this template, we entered only dyadic interactions and each agonistic interaction constituted a row. For each agonistic interaction, we entered the following information: (1) the identity of the two participants, (2) the sex of each participant, (3) whether the conflict was decided (i.e., only one opponent exhibited submissive behavior) or not, (4) the identity of the winner of a decided conflict, and (5) whether one or the other or both individuals displayed an aggressive act, an aggressive signal, a submissive act and/or a submissive signal (see **Supplementary Figure 1**).

The final dataset comprised a total of 11,499 agonistic interactions, including 5,453 interactions between females, 2,373 interactions between males, and 3,673 interactions between males and females. The majority of all agonistic interactions (10,005 or 87%) were decided. The total number of interactions per group ranged from 8 to 3,650 (mean ± SD = 479.1 ± 764.9, **Table 1**).

Indices of intersexual dominance

We computed hierarchies based on David's scores and I&SI, using the function "DS" and "ISI" of the R package "EloRating" (Neumann et al., 2011). David's score is calculated based on power relationships between individuals, and the score of each individual is calculated based on the proportion of

TABLE 1 Summary of the data collated for this study.

Species	Group	Group size	N. females	N. males	Total N. interactions	N. interactions FF	N. interactions FM	N. interactions MM
Bonobo	Ekalakala	8	5	3	387	29	120	238
	Kokoalongo	21	13	8	580	53	254	273
Chacma baboon	J_2013	27	17	10	429	255	120	54
	J_2014	27	18	9	1076	490	489	97
	L_2013	30	19	11	368	131	171	66
	L_2014	30	20	10	1467	636	674	157
Crested macaque	PB	27	18	9	459	319	79	61
	R1	51	25	26	3650	2129	837	684
Mandrill	Group 1	72	62	10	555	331	193	31
Redfronted lemur	B	12	3	9	87	5	48	34
	J	10	2	8	46	1	16	29
	X	8	4	4	82	7	60	15
Rock hyrax	Gal	6	3	3	8	0	7	1
	Isiim	21	10	11	37	14	9	14
	Suckot	18	10	8	39	15	10	14
Spotted hyena	Lemala	26	14	12	574	390	154	30
	Munge	29	13	16	195	75	63	57
Verreaux's sifaka	E	4	1	3	48	NA	20	28
	F	4	1	3	63	NA	50	13
	G	5	1	4	59	NA	50	9
Vervet monkey	BD_2016	17	11	6	203	79	66	58
	BD_2018	29	16	13	703	262	117	324
	NH_2013	16	11	5	238	131	30	77
	NH_2017	11	9	2	146	101	36	9

conflicts won and lost with other individuals in the group. For this metric, the number of conflicts is of importance because David's score does not simply provide an ordinal rank but yields power differences between individuals. However, for the purpose of our study, we only used David's score to establish individual rank order (with the highest score receiving rank 1, the second highest rank 2, etc.). One drawback of David's score is that it is relatively sensitive to the percentage of missing dyads in the matrix and to differences in observation time between individuals (Neumann et al., 2011). I&SI, on the other hand, is based on multiple iterations of randomization of the interaction matrix, until reaching the most parsimonious rank order. The advantage of this method is that it is designed to provide ordinal rank order and is less sensitive to missing data. One drawback, however, is that it may provide several equally likely rank order solutions with large datasets and in particular when interactions are lacking for a large proportion of dyads, potentially complicating the interpretation and limiting replicability. In fact, re-running the algorithm several times on the same matrices does not provide exactly the same result.

For each hierarchy, we then calculated the percentage of males dominated by each female ("the degree of female dominance") and averaged this percentage across all females to obtain two indices.

Index 1: average percentage of males in a group dominated by each female (Hemelrijk et al., 2008, 2020) using hierarchies based on male-female interactions only. This index was calculated twice, once using David's score (de Vries, 1998) to calculate the hierarchy (Index 1a) and once using hierarchies based on I&SI (de Vries, 1998, Index 1b).

Index 2: the female dominance index, FDI (Hemelrijk et al., 2020), calculated as the average percentage of males in a group dominated by each female using hierarchies based on all agonistic interactions (i.e., inter- and intrasexual conflicts). We also computed this index twice, using hierarchies based on either David's score (Index 2a) or I&SI (Index 2b).

To evaluate whether alternative estimates of the degree of female dominance or methodological differences in calculation may alter assessment of intersexual dominance relationships, we calculated three additional indices as follows:

Index 3: percentage of intersexual conflicts won by females, calculated for each female and averaged across all females.

Index 4: percentage of intersexual conflicts won by females in each intersexual dyad averaged across all intersex or something of that nature dyads.

Index 5: total percentage of intersexual conflicts won by females overall.

We then compared the correspondence among these indices by calculating pair-wise Spearman correlation coefficients for each species.

Correspondence between intra- and intersexual hierarchies

Next, we examined whether the assignment of individual rank is sensitive to the type of data used to calculate dominance hierarchies. We constructed three separate hierarchies: a female-only hierarchy based on female-female interactions only, a male-only hierarchy based on male-male interactions only, and an intersexual hierarchy based on all decided agonistic interactions. We constructed these hierarchies using David's scores since they allow for reproducibility of the analyses (i.e., the same hierarchy is obtained from the same interaction matrix each time, which is not the case with I&SI method since it is based on matrix randomization). We then extracted the ordinal dominance rank of each female (i.e., between 1 and N, N being the number of females in the group) among all other females in the intersexual hierarchy. We then calculated the Spearman rank correlation coefficient between female ordinal ranks from the intrasexual *versus* intersexual hierarchies. We repeated this process for males, yielding two correlation coefficients per group-year: one for female-only hierarchies and one for male-only hierarchies.

For all three (female-only, male-only, and intersexual) hierarchies of each group, we compiled an index of triangular transitivity, using the function "transitivity" in the R package "EloRating" (Neumann et al., 2011), which provides an index of hierarchical linearity based on the proportion of triads in the hierarchy that have transitive dominance relationships (Shizuka and McDonald, 2012). Indices below 0.75 indicate that hierarchies are less transitive than random, and an index of 1 reflects a completely transitive hierarchy. We resorted to using triangular transitivity since it is less sensitive to missing data than alternative measures of linearity (h and h′; Shizuka and McDonald, 2012; Neumann et al., 2018).

We used two separate generalized linear mixed models (GLMMs) to assess whether the degree of female dominance in a group is sensitive to differences in individual rank as a result of using either intra- or intersexual hierarchies for both, females (Model 1a) and males (Model 1b). In Model 1a, each correlation coefficient of the females' ranks between the intra and the inter-sexual hierarchy for each group-year constituted a data point; the same applies to correlation coefficients for males in Model 1b. We used separate GLMMs with beta error structure because the response in each model was bound between 0 and 1. We transformed the response using the following formula, recommended for models using a beta error distribution because it transforms zeros (which cannot be handled by beta models) into very small non-zero values (Smithson and Verkuilen, 2006):

$$x' = (x^*(N-1) + 0.5)/N$$

where x′ is the transformed value of x (here the correlation coefficient) and N the sample size.

In each model we used the degree of female dominance in the group (as expressed by Index 1a) as test predictor. Note that all five indices of intersexual dominance were found to be highly correlated (see section "Results"). We added as control predictor the percentage of male-female dyads that did not interact since this can influence David's scores (see above) and, therefore, the difference in ranks in the intra- *versus* intersexual dominance hierarchy. We could not include other control predictors, such as group size or adult sex ratio (e.g., Hemelrijk et al., 2008; Kappeler, 2017), because of our small sample size (only 21 data points in Models 1a and 24 data points in Model 1b) to avoid overparameterization. In addition to the fixed effects we added species as a random effect to account for the non-independent repeated measures on several groups of the same species.

The form of agonistic interactions in male- versus female-dominated societies

Finally, we assessed whether the degree of female dominance in a group covaries with variation in the form of agonistic interactions within and between the sexes. More specifically, we used four GLMMs to test whether the degree of female dominance influenced the likelihood of at least one of the two opponents exhibiting an aggressive act (Model 2a), an aggressive signal (Model 2b), a submissive act (Model 2c), or a submissive signal (Model 2d) in an agonistic interaction. For each model, we counted both decided and undecided agonistic interactions in which it was clear whether one or both individuals exhibited an agonistic act or signal (N = 11492 interactions). We used GLMMs with binomial error structure to model whether an act or signal was produced (Y/N) during each agonistic interaction. As test predictors, we included the degree of female dominance as quantified by index 1a, the dyad type (FF, MM, FM) and their interaction. We fitted this interaction term to test whether the effect of the degree of female dominance on the likelihood to engage in certain acts or signals differed across the three dyad types. Group size and adult sex ratio were included as control predictors in each model because they can influence social dynamics (Hemelrijk et al., 2008; Kappeler, 2017). To account for the non-independence of repeated observations involving the same individuals, dyads and species, we added the four following random effects in each model: species, identity of the

actor in the interaction, identity of the recipient and identity of the dyad. For Model 2d, the incorporation of group size as a control variable created some instability in the model preventing us from obtaining meaningful estimates for the effect of the test predictors. We therefore reran the model without group size as a variable and present the results of this second model.

While the behaviors coded as submissive acts and signals and aggressive signals were broadly similar across all the study species (see **Supplementary Materials**), the behaviors coded as aggressive acts differed for some datasets. In particular, displacement was considered an aggressive act in all datasets except two, the crested macaque and spotted hyena datasets. In the latter, displacement was only considered an aggressive act if the approaching individual expressed an aggressive signal. This divergence may reflect meaningful differences in the context and function of displacement behavior and variation in aggressiveness. To account for this different coding and to assess whether it had any impact on the conclusions drawn, we re-ran Model 2a (Model 2a bis) using a reduced dataset excluding crested macaque and spotted hyena datasets.

Statistical software and model assumption checking

We ran all statistical models in R 4.1.2 (R Core Team, 2021), using the function "glmmTMB" from the package glmmTMB (Brooks et al., 2017) for Models 1a and 1b, and the function "glmer" from the package lme4 (Bates et al., 2011) for Models 2a–2d and 2a bis. For mixed-effects models, we included the maximum random slope structure between each fixed predictor (test and control) and each random effect (Baayen et al., 2008; Barr et al., 2013). In each model, we tested for the overall significance of the test predictors by comparing the full model to a reduced model comprising all control predictors, all the random effects and random slopes, but without any test predictor, using a likelihood ratio test (LRT, Dobson, 2002). We then assessed the significance of each predictor using a LRT between the full model and a reduced model comprising all predictors except the one to evaluate. We repeated this process across all variables using the drop1 function. For each model, we tested for collinearity issues between our predictor variables using the function vif from the package "car" (Fox and Weisberg, 2011). Collinearity was not an issue (all vifs < 3). We also assessed model stability removing one level of each random effect at a time and recalculating the estimates of the different predictors that revealed no stability issue (except for model 2d, see above). Finally, we tested for overdispersion in Models 1a and 1b, which was not an issue (all dispersion parameters < 1.08). For Models 2a-d and Model 2a bis, we calculated the marginal R^2 (i.e., the variance explained by the fixed effects) and the conditional R^2 (i.e., the variance explained by the entire model including both fixed and random effects) using the function *r.squaredGLMM* of the package "MuMin" (Barton, 2020). For Models 1a and 1b we could not compile the R^2 due to negative model's distribution-specific variance.

Results

The interaction matrices compiled for this study were highly heterogeneous in terms of missing dyads, from being almost full, with most dyads interacting with each other, as in the Ekalakala bonobo group, to being largely empty, with interactions absent for $>$ 85% of dyads, as in the mandrill or rock hyrax groups (**Table 2** and **Supplementary Tables 1–3**). Most inter- and intrasexual hierarchies were highly transitive (transitivity index $\geq$ 0.97, **Tables 2** and **Supplementary Tables 1–3**), but a few hierarchies had a transitivity index close to the random level of transitivity set at 0.75 as in redfronted lemurs (group X) or well below this random level as in rock hyraxes (group Isiim) (**Table 2**). There were no strong correlations between the degree of female dominance and the degree of transitivity (correlation coefficient = 0.07, **Supplementary Figure 2**).

Indices of intersexual dominance

The species included in this comparative study represent a continuum in terms of the degree of intersexual dominance, from strictly male-dominated species as in the two chacma baboon groups (all indices $\leq$ 0.09% group males dominated by each female), to strictly female-dominated species as in the three Verreaux's sifaka groups (all indices $\geq$ 0.94, **Figures 1**, **2** and **Supplementary Table 4**). Importantly, our dataset does not comprise only species at the extreme ends of the spectrum of intersexual dominance but also several species where dominance is not very biased toward one sex (e.g., some redfronted lemur, bonobo or vervet monkey groups, **Figures 1**, **2** and **Supplementary Table 4**).

All five female dominance indices correlated strongly with each other (Spearman R2 range: 0.92–0.98, **Figures 1**, **2**), indicating that different indices of female dominance can be used interchangeably, as they do not influence the position of each group/species on the spectrum of the extent of female dominance. Please note however that for datasets with a large proportion of missing dyads the different indices provided more variable values (**Figure 2** and **Supplementary Tables 1–3**).

Correspondence between intra- and intersexual hierarchies

In models 1a and 1b, the full model was not significantly different from the null model (Model 1a: N = 21 group_years,

TABLE 2 Characteristics of the intersexual hierarchies and conflict types used in this study.

Species	Group	N dyads	Prop. Missing dyads	Transitivity (Pt)	Ratio of act vs. signal	Ratio of submissive vs. aggressive behaviors	Prop. of decided conflicts
Bonobo	Ekalakala	28	0.04	1.00	387.00	0.78	0.62
	Kokoalongo	210	0.39	0.97	64.11	0.77	0.56
Chacma baboon	J_2013	351	0.48	1.00	10.07	0.98	0.98
	J_2014	351	0.26	0.98	7.81	0.98	0.98
	L_2013	435	0.60	1.00	9.94	0.97	0.97
	L_2014	435	0.23	1.00	5.31	0.96	0.97
Crested macaque	PB	351	0.50	1.00	2.27	1.23	0.82
	R1	1275	0.45	0.98	1.43	1.84	0.85
Mandrill	group 1	2556	0.86	1.00	3.78	0.98	1.00
Redfronted lemur	B	66	0.62	1.00	NA	0.36	0.36
	J	45	0.58	1.00	NA	0.52	0.52
	X	28	0.46	0.83	NA	0.30	0.30
Rock hyrax	Gal	15	0.67	NA	1.00	1.00	1.00
	Isiim	210	0.87	0.50	1.00	1.00	1.00
	Suckot	153	0.84	1.00	1.00	1.00	0.92
Spotted hyena	Lemala	325	0.56	1.00	1.02	1.49	0.91
	Munge	406	0.73	1.00	1.17	1.57	0.87
Verreaux's sifaka	E	6	0.17	1.00	0.32	3.54	0.96
	F	6	0.17	1.00	1.00	1.13	0.87
	G	10	0.40	1.00	0.74	1.47	0.85
Vervet monkey	BD_2016	136	0.40	0.97	1.77	0.87	0.57
	BD_2018	406	0.43	0.99	2.23	0.95	0.71
	NH_2013	120	0.44	1.00	1.42	0.93	0.63
	NH_2017	55	0.16	0.97	2.46	1.34	0.88

NA: Transitivity could not be computed for the rock hyrax group Gal. For all redfronted lemurs, the ratio of act vs. signal could not be computed since no signal has been recorded in the dataset for this species.

df = 1, χ^2 = 0.096, P = 0.756; Model 1b: N = 24 group_years, df = 1, χ^2 = 1.613, P = 0.204) indicating that variable degrees of intersexual dominance did not significantly impact the differences in dominance rank observed between the intra- and the intersexual dominance hierarchy for both males and females (Supplementary Table 5 and Figure 3). These changes were rather influenced by the structure of the datasets, at least for the female hierarchies in which correlation between the intra- and the intersexual dominance hierarchies were influenced by the percentage of missing dyads (P = 0.051, Supplementary Table 5). Nevertheless, overall, intra- and intersexual hierarchies were highly correlated, across variable degrees of intersexual dominance, especially for females (Figure 3).

Differences in agonistic interactions in female vs. male-dominated societies

Individuals in most study species used acts more than signals in agonistic interactions, with some species, like redfronted lemurs and bonobos, using acts almost exclusively (Table 2). Verreaux's sifakas diverge from this general trend: they used acts and signals equally in one group and signals more often than acts in the two other groups. Together with mandrills, Verreaux's sifakas are also the study species using the highest ratio of submissive to aggressive behaviors.

The full model was significantly different from the null model in three out of four models testing the effect of the degree of female dominance and of the dyad type (M-F, F-F, M-M) on the probability of using aggressive and submissive acts or signals ($N_{interactions}$ = 11.492, N_{dyads} = 2908, $N_{individuals}$ = 508, LRT, df = 5, Model 2a: χ^2 = 34.97, $P < 0.001$; Model 2b: χ^2 = 57.25, $P < 0.001$; Model 2c: χ^2 = 8.30, P = 0.141, and Model 2d: χ^2 = 37.15, $P < 0.001$). In Model 2a investigating the probability of using aggressive acts, the interaction between the degree of female dominance and dyad type was marginally non-significant (P = 0.070, Table 3). For FM and FF dyads, the probability to use aggressive acts decreased slightly with increasing female dominance, and such decrease was steeper for MM dyads (Figure 4A and Supplementary Figure 4). We found similar results in Model 2a bis with a reduced dataset excluding crested macaques and spotted hyenas (Supplementary Figure 5) with the exception that the interaction between the degree of

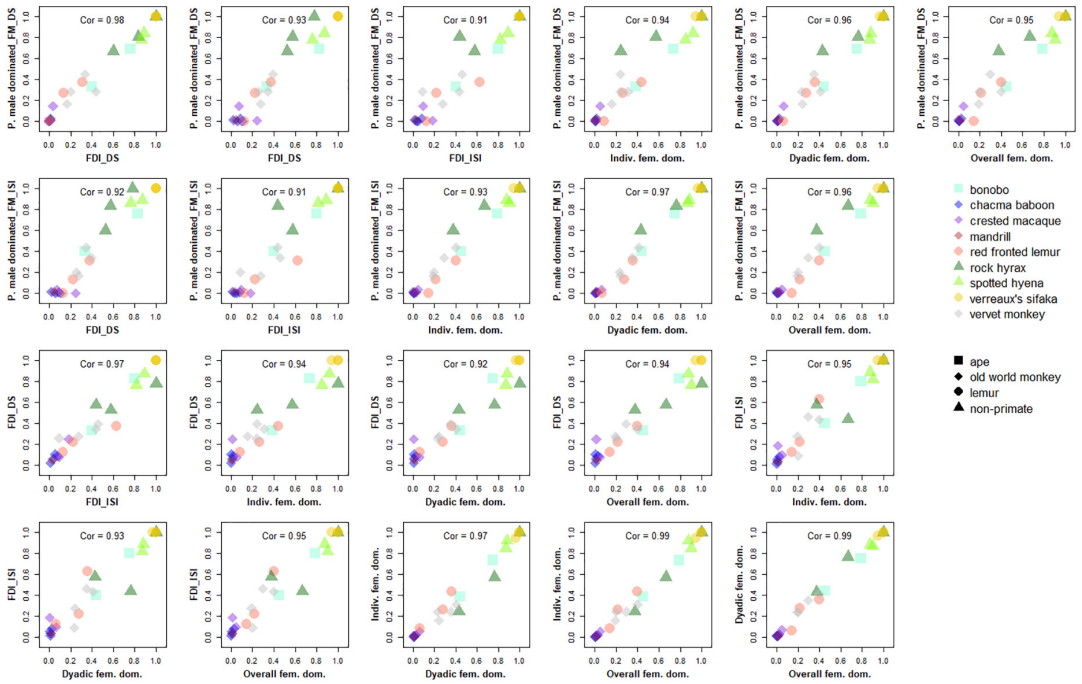

FIGURE 1
Correlations among the five female dominance indices. All pairwise comparisons among the five indices are shown, with each point representing one social group of the nine species. The 7 indices are abbreviated on the axis as follow: *P. male dominated._FM_DS:* percentage of males dominated by each female in the hierarchy compiled using David's score and based on heterosexual conflicts only (*Index 1a*); *P. male dominated._FM_ISI:* percentage of males dominated by each female in the hierarchy compiled using I&SI and based on heterosexual conflicts only (*Index 1b*); *FDI_DS:* female dominance index based on hierarchies compiled using David's score and based on all conflicts (*Index 2a*); *FDI_ISI:* female dominance index based on hierarchies compiled using I&SI and based on all conflicts (*Index 2b*); *Indiv. fem. dom.:* Individual female dominance, percentage of intersexual conflicts won by females calculated for each female and averaged across all females (*Index 3*); *Dyadic fem. dom.:* Dyadic female dominance, percentage of intersexual conflicts won by females in each male-female dyad and averaged across all heterosexual dyads (*Index 4*); *Overall fem. dom.:* Individual female dominance, percentage of intersexual conflicts won by females over males overall across all heterosexual conflicts (*Index 5*). "Cor": correlation coefficient calculated using Spearman rank correlation tests.

female dominance and dyad type was significant (P = 0.001, Supplementary Table 6) and that the probability to use aggressive acts did not decrease with increasing female dominance for FF dyads. In Model 2b, we found a significant interaction between the degree of female dominance and the probability of expressing aggressive signals (P = 0.033, Table 3). For FM and FF dyads, the probability for aggressive signals to occur in agonistic interactions decreased with increasing degree of female dominance but remained stable for MM dyads (Figure 4B and Supplementary Figure 4). In Model 2c, the degree of female dominance and dyad type did not significantly affect the probability for submissive acts to occur during agonistic interactions (Figure 4C and Supplementary Figure 4). Finally, Model 2d revealed a significant interaction between the degree of female dominance and dyad type on the probability for submissive signals to occur (P = 0.004, Table 3). While the probability for submissive signals to occur during agonistic interactions increased steadily with the degree of female dominance, this positive relationship was less pronounced for FM dyads compared to MM and FF dyads (Figure 4D and Supplementary Figure 4). The marginal R^2 were 0.142, 0.202, 0.050, 0.057, and 0.190 for Models 1a,1a bis, 1b,1c, and 1d, respectively. The conditional R^2 were 0.819, 0.608, 0.864, 0.531, and 0.907 for Models 1a, 1a bis, 1b, 1c, and 1d, respectively.

Discussion

Our study confirmed that intersexual dominance varies along a continuum from strict female dominance to strict male dominance independent of the measure used. All indices of the degree of female dominance were well correlated with each other, and the rank order among same-sex individuals was highly correlated between the intrasexual and intersexual hierarchies, and such correlation was not significantly affected by the degree of female dominance in the group. In most study groups, within sex ranks were highly correlated between the intra- and the intersexual hierarchies and variations in this correlation were function of the dataset property (i.e., % of missing dyads in Model 1a). Interestingly, the relative prevalence of each type of agonistic behavior was sensitive

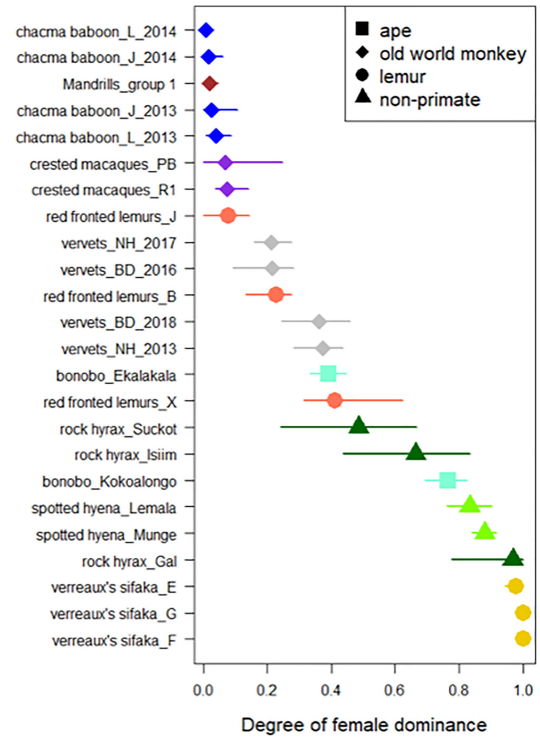

FIGURE 2
Distribution of the female dominance indices in the 24 study groups. Each line represents a study group during a given year. The symbol depicts the mean across all seven female dominance indices and the line the range of these indices. Each species is depicted with a different color. Apes, old world monkeys, lemurs and non-primates are depicted using squares, diamonds, circles and triangles, respectively.

to variation in the degree of female dominance, with more submissive signals and fewer aggressive acts being used by both sexes and across all dyad types in societies where female dominance prevails. Below, we discuss each of these main results in light of the current knowledge of heterosexual relationships across mammalian societies.

Indices of intersexual dominance

One of the novelties of the present study was the standardized application of several methods to calculate intersexual dominance across a range of mammalian species with different social systems. We found the degree of female dominance to vary continuously from strict male dominance to strict female dominance, adding to a growing number of studies (Hemelrijk et al., 2008, 2020; Rina Evasoa et al., 2019; Davidian et al., 2022; Kappeler et al., 2022) breaking with traditional binary categorizations into female-dominant vs. male-dominant species. Clearly, binary categories are insufficient to capture the variation in intersexual dominance relationships occurring both across and within species. The latter insight is illustrated by species for which we had data from more than one group, such as bonobos, redfronted lemurs and vervet monkeys, confirming results of several recent studies (Surbeck and Hohmann, 2013; Vullioud et al., 2019; Hemelrijk et al., 2020; Izar et al., 2021). These patterns open the way for future investigations of the sources of inter- and intraspecific variation in intersexual dominance patterns.

Our study will facilitate future comparative studies by demonstrating strong positive correlations among the five indices that measure the degree of female dominance. Some indices, namely 1 and 2, required the construction of intersexual hierarchies while others, namely 3–5, simply quantified the proportion of dyadic interactions won by one sex. Their high correlation suggests that they capture the same behavioral phenomenon, and validate the use of dominance hierarchies to measure asymmetries between the sexes in the propensity to win intersexual agonistic interactions. Special care should be taken for datasets with high uncertainty induced by missing interactions for a large number of dyads, as in redfronted lemurs and rock hyraxes (**Supplementary Figure 3**) for which female dominance indices varied greatly. However, even with such a variation, the study groups were positioned in the same area of the spectrum characterizing the degree of female dominance, regardless of the index chosen (**Figure 2**). Overall these indices are thus robust and consistent. This is further confirmed by the similar values generated by David's score or I&SI methods. These results indicate that all five indices capture meaningful aspects of dominance relationships between males and females, ensuring the comparability of past, present and future studies using one or several of these indices.

By positioning each study group along the intersexual dominance gradient using a standardized approach, we generated a fine-grained picture of their relative order. Such positions were largely consistent with previous descriptions of intersexual dominance for most of these species; some were already described as predominantly male dominant, like mandrills (Setchell et al., 2001), chacma baboons (Kalbitzer et al., 2015), and crested macaques (Duboscq et al., 2013; Tyrrell et al., 2020), or predominantly female dominant, like Verreaux's sifaka (Richard and Heimbuch, 1975), spotted hyenas (Vullioud et al., 2019), bonobos (Parish, 1996; Parish et al., 2000), or rock hyraxes (Koren et al., 2006; Koren and Geffen, 2009). Similarly, redfronted lemurs exhibited no sex-biased or slightly male-biased intersexual dominance as previously studied in captive and wild populations (Pereira et al., 1990; Ostner and Kappeler, 1999). The relatively balanced and flexible intersexual dominance characterizing vervet monkeys (Young et al., 2017; Hemelrijk et al., 2020) was also reported by recent studies of capuchin monkeys (Izar et al., 2021). For other groups or species, indices of female dominance contrasted with previous empirical evidence. For example, this study revealed that female dominance in bonobos is far from strict, since one group appears

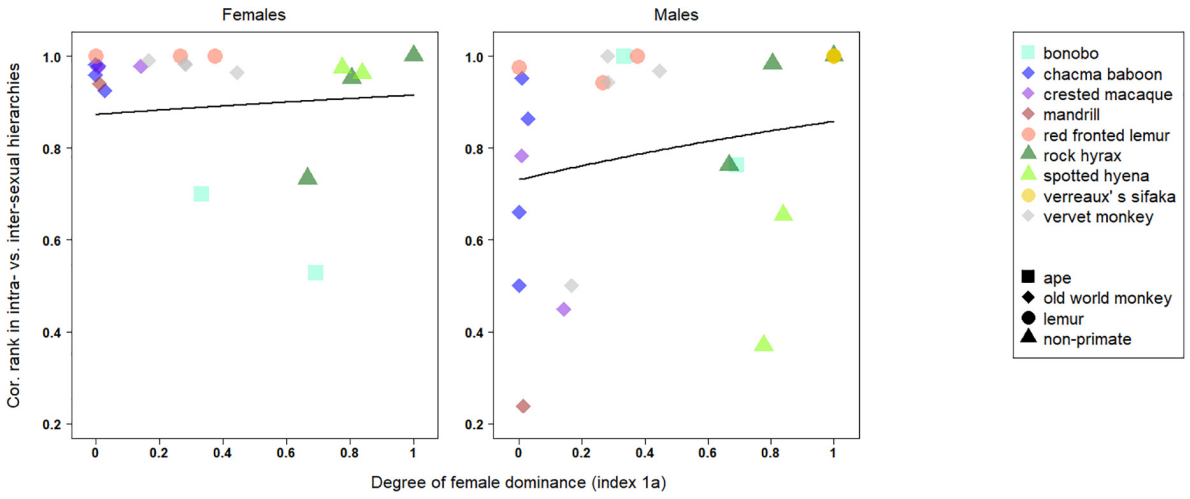

FIGURE 3
Degree of female dominance and correlation between intra- and intersexual hierarchies for females (left panel) and males (right panel). Each species is depicted using a different color. Apes, old world monkeys, lemurs and non-primates are depicted using squares, diamonds, circles and triangles, respectively. Each dot represents one study group in a given year. The black lines indicate the model's predictive lines for the effect of the degree of female dominance on the correlation between individual ranks from the intra- and from the intersexual hierarchies for females (Model 1a, left panel) and for males (Model 1b, left panel). The lines are only indicative since the *p*-values for these effects were non-significant in both models. Verreaux's sifakas do not appear in the left panel since there was only one female in each of the three groups and correlations between female ranks in the intra and intersexual hierarchies could thus not be calculated.

predominantly male dominant (**Table 3**). Generally, intersexual dominance relationships have been particularly well studied in the set of species selected for this study, but much remains to be learned about the generality of the patterns reported here from future studies of many other species and populations where social hierarchies have so far been examined separately for males and females.

Correspondence between same-sex and opposite-sex hierarchies

One cannot simply assume that an individual's position in the intrasexual hierarchy is directly predictive of its position in the intersexual hierarchy given the functional and structural differences between male and female intrasexual hierarchies (Clutton-Brock and Huchard, 2013b). Males and females often – but not always (Vullioud et al., 2019) – show distinct mechanisms of rank acquisition (de Waal, 1984; Holekamp and Smale, 1991; Foerster et al., 2016), as well as different hierarchical properties, such as steepness (Stevens et al., 2007) or stability (Holekamp and Smale, 1991). We found that in most cases, individuals maintained their same-sex dominance ordering in the intersexual hierarchy. For example, if four males are ranked A-B-C-D in the intrasexual hierarchy, it is very likely that the rank order of these males will be maintained in the intersexual dominance hierarchy, even if some females are ranked in between or above those males. This result clarifies an important aspect of the structure of intersexual hierarchies. Like intrasexual hierarchies in most species included in this study, intersexual hierarchies are mostly highly transitive (with the exception of one group of rock hyrax and one group of redfronted lemurs, **Supplementary Figure 2**). Intersexual ranks are simply obtained by merging both intrasexual hierarchies, respecting their initial order, but at variable levels, i.e., from a full entanglement, sometimes referred to as "codominance" (Lewis, 2018), to strict male or female dominance, where all members of one sex outrank all members of the other sex. The fact that the degree of female dominance was not found to influence these patterns suggests that this effect persists across the whole gradient of intersexual dominance. Overall, individuals of both sexes can thus be ordered together in a common, meaningful intersexual hierarchy, according to their competitive abilities, whatever they might be based on. While models suggest that an individual's experiences with the self-reinforcing effects of winning and losing fights may concern interactions with both males and females (Hemelrijk et al., 2008), this is not necessarily so, as indicated by evidence of a sex difference in the winner-loser effect in hamsters (Solomon et al., 2007).

A few social groups in our dataset showed a relatively low correlation between an individual's position in the same-sex *vs.* intersexual hierarchy, as in males of one chacma baboon group, or in females of one bonobo, one crested macaque and one rock hyrax group (**Figure 3**). It is possible that the number of dyads for which no interaction was recorded may affect the robustness of hierarchies. Yet, this is unlikely to explain our results given that the percentage

TABLE 3 Effect of the degree of female dominance and dyad type (FM, FF, MM) on the probability of using aggressive acts (Model 2a), aggressive signals (Model 2b), and submissive signals (Model 2d).

Model	Response	Predictor	Estimate	SE	CI_{low}	CI_{high}	$\chi 2$	P
2a	Did the conflict comprise an aggressive act (Y/N)	Intercept	2.37	1.25	−0.17	5.03		
		Dyad type (FM)	0.51	0.11	0.18	0.83		
		Dyad type (MM)	−0.12	0.17	−0.56	0.29		
		Degree of female dominance	−0.17	0.49	−0.97	0.82		
		Sex ratio[§]	−1.24	0.19	−1.87	−0.69	38.41	**<0.001**
		Group size[§]	−0.88	0.23	−1.58	−0.26	15.70	**<0.001**
		Female dominance * dyad type (FM)	−0.18	0.10	−0.53	0.15	5.31	0.070
		Female dominance * dyad type (MM)	−0.29	0.13	−0.71	0.12		
2b	Did the conflict comprise an aggressive signal (Y/N)	Intercept	−1.22	1.51	−4.74	1.76		
		Dyad type (FM)	0.41	0.13	0.01	0.77		
		Dyad type (MM)	−0.95	0.23	−1.54	−0.37		
		Degree of female dominance	−0.87	0.51	−1.88	−0.06		
		Sex ratio[§]	−0.05	0.22	−0.72	0.67	0.04	0.848
		Group size[§]	0.49	0.27	−0.24	1.20	3.23	0.072
		Female dominance * dyad type (FM)	0.22	0.13	−0.13	0.60	6.85	**0.033**
		Female dominance * dyad type (MM)	0.57	0.19	0.08	1.05		
2d	Did the conflict comprise a submissive signal (Y/N)	Intercept	−4.81	1.83	−9.34	−1.11		
		Dyad type (FM)	0.19	0.45	−1.02	1.27		
		Dyad type (MM)	1.20	0.88	−1.06	3.09		
		Degree of female dominance	2.90	0.79	1.87	4.23		
		Sex ratio[§]	0.46	0.41	−0.32	1.34	1.18	0.278
		Female dominance * dyad type (FM)	−0.56	0.27	−1.34	0.18	11.08	**0.004**
		Female dominance * dyad type (MM)	−0.48	0.50	−1.61	0.76		

Results from Model 2c explaining the probability of using submissive acts are not shown here as this model did not differ from the null model. Since all the continuous variables were standardized to a mean of 0 and a standard deviation of 1, the intercepts and corresponding main effects are indicated for an average degree of female dominance, sex ratio and group size. For all the estimates of the "Dyad type" fixed effect, female-female dyads are the reference category. SE indicates the standard error of the estimate for each predictor. [§]Indicates control predictors. Significant p-values ($p < 0.05$) are indicated in bold and trends ($p < 0.1$) in italics. CI_{low} and CI_{high} indicate the lower and upper limits of the 95% confidence intervals for the estimates of each predictor. The sample size for each model is $N_{interactions} = 11492$, $N_{dyads} = 2908$, $N_{individuals} = 508$.

of missing dyads was included as a control factor in our models and did not yield a significant effect on the correlation between the two hierarchies. In addition, there are species and sex differences in the dynamics of hierarchies that are not accounted for here, and which may influence hierarchical properties, especially transitivity. Specifically, the methods used here to build hierarchies ignore temporal changes in hierarchies, whereas other methods continuously adjust and update a hierarchy over time when it is characterized by high temporal dynamics (e.g., use of the dynamic Elo-ranking methods: Neumann et al., 2011). Static approaches may be suitable in some cases, such as the stable, linear and heritable hierarchies of female cercopithecines, but less so for unstable male hierarchies in seasonal breeding species where most males are not permanent group members, as in mandrills (Brockmeyer et al., 2015) and rock hyraxes (Barocas et al., 2011), or species where males move frequently between groups, as in crested macaques (Neumann et al., 2011; Marty et al., 2016). The moderate correspondence between intra- and intersexual hierarchies may thus reflect the social dynamics in these species, which may occur over the course of a year (i.e., the time frame used here to derive hierarchies).

Different dominance styles in male- and female-dominated societies

We finally investigated whether the relative importance of agonistic acts vs. signals and of aggressive *vs.* submissive behavior varies across the spectrum of interspecific variation in intersexual dominance. This analysis highlighted at least two important results. First, the relative frequencies with which different agonistic behaviors were used followed the same pattern in relation to the degree of female dominance for male-male, female-female, and male-female dyads. Second, and most noticeably, an increase in the degree of female dominance was related to a steep increase in submissive signals during contests and a modest decrease in the use of aggressive acts. This pattern suggests that in societies where dominance is biased toward females, signals are particularly important for structuring social life and likely limit the use of direct aggression during conflicts,

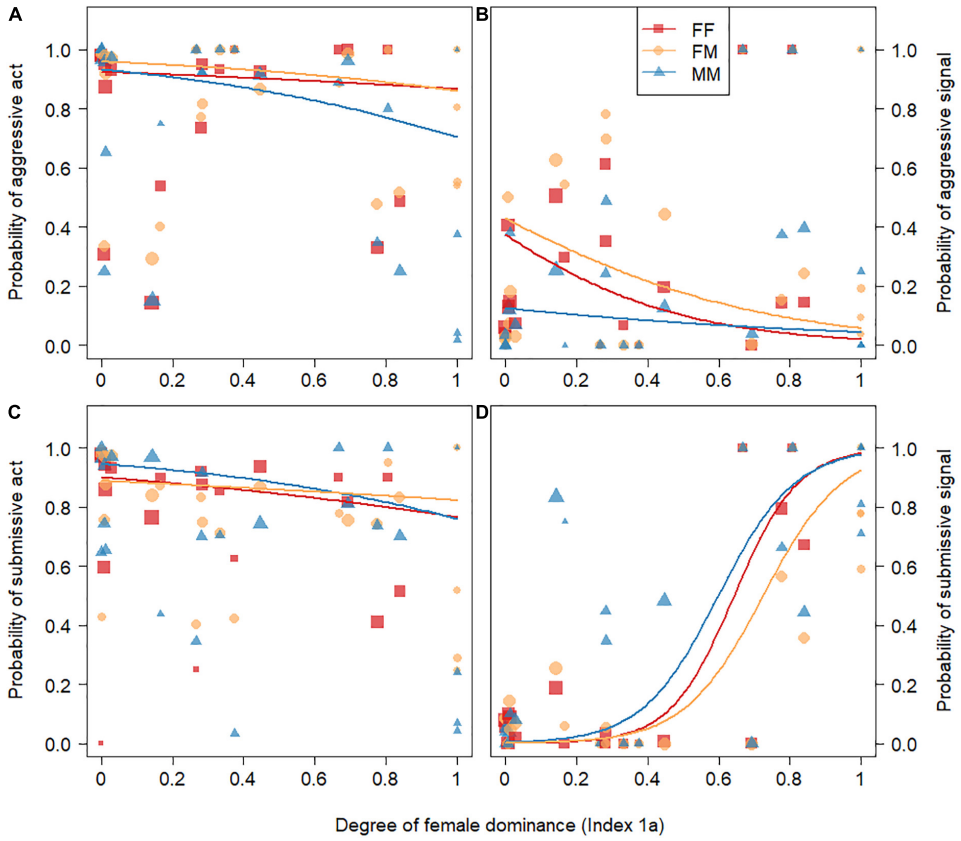

FIGURE 4
Influence of the degree of female dominance (Index 1a) and dyad type (FM, FF, MM) on the likelihood for conflicts to comprise aggressive acts **(A)**, aggressive signals **(B)**, submissive acts **(C)**, or submissive signals **(D)**. Each dyad type is depicted using a different color and symbol: Red square: female-female dyads (FF), orange circle: female-male dyads (FM) and blue triangle: male-male dyads (MM). Each dot represents one dyad type of a study group on a given year and dot size is proportional to the log number of dyads. Log scale was chosen here because the number of dyads in each dyad type in the largest groups were orders of magnitude larger than in smallest groups. The red, orange and blue lines depict the predicted relationship between the degree of female dominance and the likelihood of each act or signal to occur for FF, FM, and MM dyads respectively. These lines are derived from Models 2a (panel **A**), 2b (panel **B**), 2c (panel **C**), and 2d (panel **D**). Please note that for Model 2c the full model did not significantly differ from the null model and the corresponding lines do not represent meaningful statistical relationships but are used for illustration.

compared to societies dominated by males. Nonetheless, the intensity and frequency of agonistic acts or signals can vary even between species that are positioned alongside on intersexual dominance spectrum. For example, across macaque societies, which are all largely male-dominated, there are well-described differences between species in the ratio of contact aggression and non-contact aggression, which are typically related to a species' "dominance style," which characterizes dominance relationships from most egalitarian to most despotic (Thierry, 2007).

The relationship between the degree of female dominance and the differential use of aggression and submission might partly reflect a reduction in male aggressiveness across the female dominance gradient, along with a decreasing magnitude of sexual dimorphism. Indeed, in several species where females dominate males, their body size or levels of aggressiveness and androgens resemble those of males – as in many lemurs (Jolly, 1984; Petty and Drea, 2015; Grebe et al., 2019), spotted hyenas (McCormick et al., 2021), rock hyraxes (Koren et al., 2006), and meerkats (Davies et al., 2016), and ongoing research confirms that the degree of sexual dimorphism is a strong predictor of the outcome of intersexual agonistic interactions across primates (Huchard et al., unpubl. data). In addition, species-specific patterns of agonistic interactions (**Supplementary Figure 2**) suggest that the general, interspecific relationship is largely driven by spotted hyenas and sifakas, which stand out by using fewer aggressive acts than other female-dominant species. In contrast, the increased use of submissive signals in female-dominant species is robust and involves most populations where dominance is largely female-biased, except for bonobos. Overall, female-biased dominance appears associated with a higher ratio of submissive signals to aggressive acts, a result that needs verification with a larger number of species, as well as using analyses that control for phylogenetic proximity between species. Controlling for

phylogeny was here complicated by the low number of species involved, coupled with a heterogeneous phylogenetic coverage comprising a disproportionate number of primates as well as a couple of other, distantly related species.

The generality of this phenomenon across all dyad types may be compatible with the idea that agonistic interactions are ruled by convention-based norms that are shared by group members across age-sex-classes. These norms might possibly be socially transmitted, or flexibly influenced by prior experience, such as winner-loser effects (Tibbetts et al., 2022). Regardless of the underlying mechanism, these results suggest that female-dominated societies may rely less on aggression than male-dominated ones. This constitutes an important finding to identify the consequences of intersexual power for individual health, welfare and fitness, as well as for social dynamics and population demography. Our findings may also have ramifications for a better understanding of variation in the level of intra- and intersexual violence across past and contemporary human societies (Gómez et al., 2016; Glowacki et al., 2020).

Other patterns are more discrete. The use of aggressive signals also covaried with the degree of female dominance in female-female and intersexual dyads, with fewer threats observed in societies where ritualized submissive signals limit the use of direct aggression; threats may therefore lose their intimidating function when they are not reinforced by direct aggression. Alternatively, it is possible that either aggressive or submissive signals are needed to maintain a dominance hierarchy (Tibbetts et al., 2022), but that both are functionally redundant and rarely co-exist. Male-male dyads, in contrast, hardly use any threats across the continuum, possibly because it is risky to threaten a rival in male-dominant societies where male-male competition is often intense and contest-based, while threats are uncommon in female-dominant societies for the reasons discussed above. Finally, the slight (non-significant) decline of submissive acts along the female dominance gradient likely reflects the decline of aggressive acts, probably because submissive acts represent responses to aggressive acts. In contrast, aggressive acts are not systematically followed by a submissive act, which may explain why the decline is less pronounced for submissive than aggressive acts.

Conclusions and Recommendations

This study provides important insights and key methodological tools to study intersexual dominance relationships in mammals, and perhaps in other vertebrates. First, we show that several distinct quantitative indices of intersexual dominance are equally successful at ordering groups from several populations and species along an intersexual gradient ranging from strict male to strict female dominance. Second, we show that intersexual hierarchies are meaningful emergent properties of interactions occurring within and between the sexes. These hierarchies arise from merging male and female hierarchies, where individuals retain their intrasexual rank, but can be outranked by a variable number of opposite-sex group members. Third, we found continuous variation in patterns of agonistic interactions across species, characterized by less direct aggression and more ritualized submissions in female-dominant societies, which have apparently developed potent mechanisms of conflict mitigation that promote peaceful interactions and inhibit aggression. This work provides important foundations for future studies of intersexual dominance across mammals to uncover determinants and consequences of variation in intersexual dominance comprehensively, using standardized, quantitative measures within and across societies.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Data deposited in Figshare: https://figshare.com/articles/dataset/Dataset_for_Sex_and_Dominance_How_to_Assess_and_Interpret_Intersexual_Dominance_Relationships_in_Mammalian_Societies_/19583215.

Ethics statement

This study uses data from nine different species coming from countries with different regulations. All details regarding permits and authorizations have been provided in the relevant section of the manuscript.

Author contributions

The manuscript was conceived collectively based on shared discussions among co-authors during a workshop that took place in 2020 in Leiden (Netherlands), co-organized by CH and PK. PK, EH, and CG-B drafted the manuscript. CG-B performed the data analyses. All authors contributed critically to writing, either collected, curated, and/or analyzed the behavioral data (from their respective study population).

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.918773/full#supplementary-material

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How to measure intersexual dominance?

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Intersexual dominance (dominance between the sexes) is often assumed to be binary with species categorized as either male- or female-dominant. Yet in many species, the degree of intersexual dominance falls somewhere in the middle of these two extremes. There are several measures of intersexual dominance, but in empirical studies, it is not possible to evaluate which is best because the real degree of intersexual dominance is unknown. This evaluation is possible, however, in the agent-based model, DomWorld, because individuals have internal dominance values that drive their agonistic behavior. In the present study, we defined the accuracy of measures of intersexual dominance in DomWorld by the strength of the correlation between the degree of intersexual dominance based on A) their internal dominance values and B) observations of their competitive interactions (similar to observations in empirical studies). We examined the four measures that have been most commonly used in the literature: the proportion of intersexual conflicts won and initiated, the Female Dominance Index, and the proportion of female-dominant dyads. The Female Dominance Index was highly accurate, possibly because it was based on the outcomes of intra- and intersexual conflicts, both of which influence an individual's dominance. The proportion of intersexual conflicts initiated was similar in its accuracy to the Female Dominance Index and it was the only measure to be unaffected by missing data. Measures were more accurate when groups were smaller, or the intensity of aggression was higher, but their accuracy did not depend on the degree of sexual dimorphism. To best represent dominance relations between the sexes, we recommend reporting both the Female Dominance Index and the proportion of intersexual conflicts initiated.

KEYWORDS

intersexual dominance, Female Dominance Index, dominance, sex, winner-loser effect, DomWorld, agent-based model

Introduction

Dominance relations among individuals result from repeated agonistic interactions (Drews, 1993). An individual that consistently defeats an opponent (evokes submission) is dominant, while the victim is subordinate (Drews, 1993). Dominance hierarchies function to reduce the frequency of conflicts because individuals are unlikely to attack if they think they will be defeated (Jackson, 1991). The dominance style of a group ranges on a continuum from despotic to egalitarian (Vehrencamp, 1983). In groups where the difference in winning ability among individuals is high, the dominance style is more despotic, and more

dominant individuals gain greater access to monopolisable resources such as food, space, or mates by outcompeting less dominant individuals (Vehrencamp, 1983). When the winning ability among individuals in a group is similar, the dominance style of the group is more egalitarian and all individuals have similar access to resources (Vehrencamp, 1983). Thus, the dominance style of a group as well as the dominance rank of an individual are important to its fitness and survival.

Prior attributes such as body size are often reported to underlie the ability of one individual to defeat another (Chase and Seitz, 2011). Thus, in species where males are larger than females, males are often assumed to be dominant over all females. Yet, in some species with male-biased sexual dimorphism, females dominate some males despite their smaller body size [e.g., bonobos (Surbeck and Hohmann, 2013), vervets (Hemelrijk et al., 2020), capuchins (Izar et al., 2021), macaques (Hemelrijk et al., 2008), rock hyraxes (Koren et al., 2006), wolves (Cafazzo et al., 2016), and giraffes (Horová et al., 2015)]. Therefore, prior attributes are not the only aspect that influences dominance. Other factors also influence an individual's ability to win a fight, such as support from others in conflicts (White and Wood, 2007), leverage (Lewis, 2002), and prior experience (Hsu et al., 2006).

The winner–loser effect implies that in their subsequent dominance interaction, winners are more likely to win again, and losers are more likely to lose again. The winner–loser effect has been found in many taxa ranging from crustacea, amphibia, and insects to mammals including humans (Hsu et al., 2006). In empirical studies, it has been shown to (partially) underlie the formation of dominance hierarchies (Franz et al., 2015) and in theoretical studies, dominance hierarchies similar to those of real animals emerge based on winner–loser effects (Chase, 1974; Beacham, 1988; Hemelrijk et al., 2017). The effect has been demonstrated in same-sex dyads, hermaphroditic dyads, and when the sex is unknown (Hsu et al., 2006; Mesterton-Gibbons et al., 2016) but has been studied seldom between the sexes because studies of intersexual dominance are lacking in comparison to studies on intrasexual dominance. Generally, dominance relations are studied separately for each sex because males and females are supposed to have different drivers underlying competition; males compete for access to females and females compete for access to food (Trivers, 1972). Yet, clearly, males can act as a direct competitor for food and space with females (Li and Kokko, 2019).

Whether individuals that engage in intersexual conflicts experience the winner–loser effect has seldom been studied, although there is indirect evidence suggesting that they do. The winner–loser effect was demonstrated in dominance interactions between pigs where half of the dyads were mixed sex (Oldham et al., 2020). Also, in crickets, males that previously won a conflict were more likely to attack a female than males that had not fought (Adamo and Hoy, 1995), suggesting the winner–loser effect can be carried over from intrasexual to intersexual conflicts. Besides, in some agent-based models, where the winner–loser effect is made to operate both within and between the sexes, patterns emerge that resemble empirical patterns (Hemelrijk et al., 2017; Hofstede et al., 2018). Therefore, the winner–loser effect may be functioning in interactions between the sexes as well as within a sex. Winning a conflict against a member of the same sex may influence an individual's ability to win a conflict against a member of the opposite sex and *vice versa*. Regarding intrasexual dominance hierarchies, while they are normally calculated using only intrasexual conflicts, they may be more accurate if they also included intersexual conflicts because these provide more information about an individual's prior experience.

Species have often been grouped arbitrarily in categories of either "male-dominant" or "female-dominant." Yet, intersexual dominance in a group is seldom binary. Rather, groups may range from strongly male-dominant to strongly female-dominant (Davidian et al., 2022; Kappeler et al., 2022b). For instance, strict female dominance over males was supposed to be widespread in lemurs, but intersexual dominance relations have been shown to vary across groups and species, when they were measured as the proportion of intersexual conflicts won and the proportion of subordinate males (Kappeler et al., 2022a). What remains unclear is which measure of intersexual dominance best represents dominance relations between the sexes in groups of animals. A study by Kappeler et al. (2022b) demonstrated that the degree of intersexual dominance strongly correlated among several measures of it, suggesting that all measures were equally suitable. However, in empirical studies, the accuracy of measures cannot be determined because there is no "true" value of intersexual dominance with which the degree of intersexual dominance based on observed conflicts can be compared. Indeed, several traits such as group size, dominance style, or a higher proportion of unknown relations have been shown to bias the results of measures of dominance (Hemelrijk et al., 2005; Klass and Cords, 2011; Douglas et al., 2017; Sánchez-Tójar et al., 2018), although it is unclear how they influence measures of intersexual dominance. While the accuracy of measures of intersexual dominance cannot be estimated in empirical data, it can be studied in a computational model, DomWorld, because here both are known: the internal dominance of individuals that influences their behavior as well as their observed competitive interactions (Hemelrijk, 1999).

In the agent-based model, DomWorld, patterns of behavior resemble those observed in real animals (Hemelrijk et al., 2017). In it, individuals are guided by simple rules to group and compete. The outcomes of their competitive interactions are self-reinforcing. Individuals have internal dominance values that determine their likelihood to attack and win conflicts and, thus, reflect their real dominance. After a conflict, the dominance value of the winner is increased (making it more likely to win again) and that of the loser is decreased (making it more likely to lose again), representing the winner–loser effect

(Hsu et al., 2006, 2009). In the model, the internal dominance value of an individual steers its behavior and is thus considered the "real" dominance that cannot be known in empirical studies. Data are collected in a similar way on the competitive interactions in the model as in real animals. Thus, in the model, the accuracy of different measures of intersexual dominance can be determined by comparing the intersexual dominance values based on the "real" internal values with those based on observed conflicts.

DomWorld is suitable for this type of analysis for several reasons. First, patterns of social behavior emerge in the model that resemble those of real animals, including patterns of intersexual dominance which have been confirmed in empirical studies (Hemelrijk et al., 2008, 2020; Izar et al., 2021). Namely, it has been shown that females are dominant over more males if there is a higher proportion of males in the group because frequent male–male aggression causes some males to become victimized and over these males, females are dominant. Second, DomWorld has previously been used to determine the accuracy of different methods of deriving a dominance hierarchy by comparing a hierarchy based on observed outcomes of conflicts to the hierarchy based on internal dominance values (Hemelrijk et al., 2005). Third, in the model, different group sizes, sex ratios, dominance styles, and degrees of sexual dimorphism can be simulated and the effects of each of these traits can be studied in relation to the accuracy of measures of intersexual dominance.

In the present paper, we study the accuracy and robustness of measures of intersexual dominance using the agent-based model, DomWorld. We first conduct a literature review to find which measures of intersexual dominance are used most often. Subsequently, we investigate in the model the accuracy of four of these measures. We study how their accuracy is affected by traits such as dominance style, group size, and sex ratio. We examine the robustness of measures by investigating whether the measures are unaffected by reducing the dataset, thus by introducing a higher proportion of unknown relationships (where two individuals do not interact). We examine also whether intrasexual dominance hierarchies based on observed interactions resemble the real dominance relations within a sex (based on internal values) more strongly if the hierarchy is calculated using either only intrasexual conflicts or both intrasexual and intersexual conflicts.

Materials and methods

For clarity and conciseness from hereon, we consider measures of intersexual dominance from a female perspective, but the male perspective can be calculated as the inverse, e.g., if the proportion of intersexual conflicts won by females is 20%, this means it is 80% for males.

Literature review

In August 2021, LS searched the Web of Science for measures of intersexual dominance, under the keywords "female dominance" (419 results) and "inter-sexual OR intersexual dominance" (16 results). Seventy-five papers were found that used a quantitative measure of intersexual dominance 141 times. Disregarding whether measures were used repeatedly by the same authors or research group, we considered only measures that quantified patterns of dyadic agonistic interactions between males and females, and excluded measures concerning coalitions, affiliation, leadership, and feeding priority. We preserved the definitions used in the papers and focused on the measure of intersexual dominance. Thus, if two papers use the measure "the proportion of intersexual conflicts won" but defined winning differently, we counted them as the same. We included studies both in the wild and in captivity. We considered studies of animals in natural settings (groups in captivity or the wild) as well as in artificial settings (e.g., test arenas). We sorted the 141 measures into 22 distinct categories, combining similar measures (Table 1). Eight measures that were only used once are not shown. Refer to the Supplementary material for an exhaustive list.

We selected the most common measures, including only those used more than five times since these made up 80% of the times that measures of intersexual dominance were used. We did not use measures that compared frequencies of aggression or submission between males and females because (1) they treat intersexual dominance as a dichotomy and (2) a higher frequency of aggression is not necessarily indicative of dominance. The final measures of intersexual dominance chosen were the proportion of intersexual conflicts won, the Female Dominance Index, the proportion of female-dominant dyads, and the proportion of intersexual conflicts initiated.

Description of measures

The proportion of conflicts won or initiated was calculated per female for all their conflicts against males and then averaged over all females. The proportion of female-dominant dyads was calculated as the proportion of intersexual dyads where females dominated males (won more than 50% of conflicts) divided by the total number of intersexual dyads where a male and female had at least one interaction. Here, we defined a female-dominant dyad as females winning more than 50% of conflicts against a male, but in the literature, there were different definitions of a "female-dominant dyad" such as if females won more than 50% of conflicts (e.g., Hohenbrink et al., 2016), more

TABLE 1 Distinct categories of quantitative measures of intersexual dominance.

#	Measure	Number of times published
1	**Proportion of intersexual conflicts won by females**	**36**
2	**Relative rank order or Female Dominance Index***	**27**
3	Frequency of intersexual conflicts initiated by males and females	20
4	Frequency of aggression initiated by males and females	14
5	**Proportion of female-dominant dyads**	**8**
6	**Proportion of intersexual conflicts initiated by females**	**8**
7	Frequency of aggression received by males and females	3
8	Frequency of intersexual conflicts won by males and females	3
9	Frequency of submission by males and females	3
10	Sex of the highest-ranking individual	3
11	Average rank of males vs. females	2
12	Frequency of intersexual submission by females	2
13	Proportion intersexual conflicts won that were initiated by females	2
14	Proportion of all conflicts initiated by females	2

The measures studied in this paper are in bold. "Conflict" refers to an agonistic interaction that has a winner but does not necessarily involve aggression. "Aggression" refers to an individual aggressing another but does not consider the behavior of the receiver.
*Some studies describe the position of males and females in the dominance hierarchy relative to each other. We combine these with the Female Dominance Index since they describe the same pattern.

than 75% conflicts (e.g., Knowles et al., 2004), or significantly more conflicts than 50% (binomial test) (e.g., Hasiniaina et al., 2018). We chose the threshold of more than 50% to make the measure more comparable to our other measures of intersexual dominance that do not allow for frequent "neutral" dyads i.e., those that are neither male- nor female-dominant.

The Female Dominance Index (Hemelrijk et al., 2008) is the average proportion of males that females are dominant over in a group, based on a hierarchy of all adults (constructed from wins and losses). Based on this hierarchy, the Female Dominance Index is the total number of males that each female outranks, divided by the maximum number of males females could dominate (number of females in a group multiplied by the number of males in a group). If a female ties with a male in her dominance rank, this is counted as 0.5 dominance of the female over the male. This results in a Female Dominance Index value that is the average proportion of males that females dominate. Because the Female Dominance Index is affected by how the dominance hierarchy is calculated, we studied four popular methods of deriving a hierarchy and calculated Female Dominance Index based on each: David's score Dij method (DS) (Gammell et al., 2003; de Vries et al., 2006), Average Dominance Index (ADI) (Hemelrijk et al., 2005), I&SI (de Vries, 1998), and randomized Elo-rating (Sánchez-Tójar et al., 2018). For randomized Elo-rating, we kept the parameters used in Sánchez-Tójar et al. (2018) meaning the sigmoid parameter was set as 0.01 and k was set as 200, and we randomized the order of interactions 1,000 times. For further details on how these dominance hierarchies are calculated, refer to Supplementary material.

DomWorld

Here, we summarize the main aspects of the agent-based model, DomWorld. For a full description of the model, see Hemelrijk (1999). In DomWorld, agents are guided by cognitively simple rules to move, group, and compete. All agents begin the simulation with an initial DOM value (Table 2) that influences their likelihood to engage in and win conflicts and is updated following conflicts. Individuals compete over non-specified resources and have a risk-sensitive attack strategy (Jackson, 1991; Hemelrijk, 2000). This strategy means that an individual will only attack if it thinks it will win a conflict (so-called "mental battle"). An individual is more likely to start a conflict if it is more dominant than its partner i.e., has a higher DOM value. The probability to win by agent i is calculated as its DOM value divided by the sum of the DOM values of both partners (DomRatio, Equation 1). If it thinks it will win, thus, if this ratio is higher than a random number between 0 and 1, it will initiate a "real" fight. Whether an individual wins ($w_i = 1$) or else loses ($w_i = 0$) a real fight is calculated in the same way.

$$w_i \begin{cases} 1 & \dfrac{DOM_i}{DOM_i + DOM_j} > RND\,(0,1) \\ 0 & else \end{cases} \quad (1)$$

Following a conflict, the winner turns toward the loser, chases it a *ChaseDist, and* the loser turns 180° and flees a *FleeDist*. The DOM value of the winner increases and the loser decreases by the same amount (Equation 2). The amount with which the DOM value of both partners is updated following a conflict depends on the rank distance between them and the intensity of aggression (StepDom) of the initiator; a more unexpected result or higher value of StepDom causes a larger update to dominance

TABLE 2 Parameters in experiments in DomWorld.

InitDom		StepDom		Intensity of aggression	Group size	Percentage of females
Females	Males	Females	Males			
					10	30, 50, 70
24	24	0.5	0.5	Medium	20	25, 50, 75
					30	27, 50, 73
					10	30, 50, 70
16	32	0.8	1	High	20	25, 50, 75
					30	27, 50, 73
					10	30, 50, 70
16	32	0.1	1	Medium	20	25, 50, 75
					30	27, 50, 73
					10	30, 50, 70
16	32	0.05	0.5	Low	20	25, 50, 75
					30	27, 50, 73

InitDom is the DomValue with which individuals are initiated; StepDom represents the intensity of aggression of females and males; sex ratio is indicated as the percentage of females in the group.

values than an expected result or a lower value of StepDom.

$$DOM_i := DOM_i + \left(w_i - \frac{DOM_i}{DOM_i + DOM_j}\right) * STEPDOM_i$$

$$DOM_j := DOM_j - \left(w_i - \frac{DOM_i}{DOM_i + DOM_j}\right) * STEPDOM_i \quad (2)$$

Experimental setup and analyses

The internal and observed degree of intersexual dominance

Time in the model is based on activations, with 20 activations of all individuals equating to one period. We use data in the model after a stable dominance hierarchy has developed, namely from periods 230 to 260. The degree of intersexual dominance based on internal dominance values was calculated per individual as its average DOM value over this time period. A dominance hierarchy was created based on these values by ordering them from largest (most dominant) to smallest (least dominant). Based on this internal hierarchy, we calculated the average proportion of males that females dominant (Female Dominance Index, Hemelrijk et al., 2008). We measured the observed degree of intersexual dominance by observing the competitive behavior of individuals and calculated the different measures as described above.

Parameters in experiments

We ran simulations with different parameters for the initial dominance (InitDom) and intensity of aggression (StepDom) of the sexes, resembling either sexually dimorphic or monomorphic species (Table 2). Although we label individuals "Male" and "Female," the only difference between them is their InitDom and StepDom and thus a simulation with male-biased sexual dimorphism is equivalent to one with female-biased sexual dimorphism. For a full list of parameters, refer to Supplementary Table S1.

We simulate four different types of societies based on the intensity of aggression of males and females (StepDom) (Table 2). We do not use very low values for StepDom (e.g., Female StepDom = 0.01, Male StepDom = 0.1), because this results in a group where all males always dominate females (Hemelrijk et al., 2008). We also investigate how group size and sex ratio (Table 2) influence the accuracy of measures.

Accuracy

For each of the 36 parameter settings, we ran the model 40 times. Per run, we estimated the accuracy of measures of intersexual dominance by correlating each of the different measures based on observed behavior with the internal degree of intersexual dominance using a Spearman correlation. Regarding the Female Dominance Index, we examined which of the four ways chosen for deriving a hierarchy (DS, ADI, I&SI, and randomized Elo-rating) resulted in the strongest correlation with internal values.

We studied whether we derived intrasexual hierarchies (hierarchies of a single sex) more accurately when using only intrasexual conflicts or both intra- and intersexual conflicts.

We calculated intrasexual dominance hierarchies of males and females separately based on how often individuals won from members of the same-sex (intrasexual conflicts) or members of both sexes (both intra- and intersexual conflicts). We correlated the ordinal rank position of individuals in the hierarchy relative to members of their own sex with their position in the hierarchy based on internal DOM values using a Spearman correlation.

Robustness

We determined the robustness of measures of intersexual dominance in terms of their insensitivity to data reduction. Omitting dominance interactions causes a higher proportion of unknown relationships, which is known to affect other measures of dominance (Klass and Cords, 2011). Here, for each parameter setting, we omitted 0, 5, 10, 15, 20, and 25 periods uniformly chosen between periods 230 and 260 for each of the 40 runs. For each number of omitted periods, we calculated the four measures of intersexual dominance based on observed behavior per run and correlated these values of intersexual dominance with the proportion of missing data using a Spearman correlation. When values of intersexual dominance were less affected by missing data, they were considered more robust.

Statistical analyses

Data manipulation and statistical tests were conducted in R (version 4.1.2) (R Core Team, 2021) and RStudio (RStudio Team, 2020). Graphs were created in Rstudio with ggplot2 (v3.3.6; Wickham, 2016) and ggpubr (v0.4.0; Kassambara, 2020). Hierarchies created using DS and I&SI were done so using the EloRating package for R (v0.46.11; Neumann and Kulik, 2020). Hierarchies based on randomized Elo-rating were calculated with the aniDom package in R (v0.1.5; Farine and Sánchez-Tójar, 2021). We assessed the normality of data using Shapiro-Wilk tests and based on the inspection of qq plots. Data were non-normal, and thus, we used non-parametric tests (Friedman test and Wilcoxon signed-rank test with Holm adjusted *p*-values).

We studied which factors influenced the accuracy of measures by fitting a general linear model using the glmmTMB package (v1.1.3; Brooks et al., 2017). Since the response variable was the correlation coefficient (non-integer) and our data was bounded between 0 and 1, we use a beta family. The goodness of fit was measured through statistics based on simulated residuals from the package DHARMa (v0.4.5; Hartig, 2022). We checked for co-linearity in multi-variate models using the variance inflation factor (VIF). For the significance of factor variables, we report the likelihood ratio test between the full model and the model without the factor of interest and provide full summary tables in the Supplementary material. We performed *post-hoc* pairwise comparisons using the emmeans package (v1.7.4.1; Lenth, 2021) to compare the estimated marginal means among factors (*p*-values here were corrected for multiple comparisons using the Tukey method).

Results

Female Dominance Index

The Female Dominance Index is the average proportion of males that females dominate in a dominance hierarchy. When the dominance hierarchy based on observed wins and losses was calculated using DS, the Female Dominance Index was more strongly correlated with the degree of intersexual dominance based on internal dominance values than when the hierarchy was calculated using ADI, I&SI, and randomized Elo-rating [*Friedman test:* $X^2_{(3)} = 93.33$, $p < 0.001$; DS vs. ADI $p < 0.001$; DS vs. ISI $p < 0.0001$; DS vs. Elo-rating $p < 0.0001$; ADI vs. ISI $p < 0.0001$; ADI vs. Elo-rating $p < 0.0001$; ISI vs. Elo-rating $p < 0.0001$, Figure 1A]. Thus, from hereon, we use DS to calculate dominance hierarchies.

When studying dominance among same-sex individuals, the position of individuals in a hierarchy relative to members of their own sex (intrasexual hierarchy) was more strongly correlated with the internal dominance hierarchy when both intra- and intersexual conflicts were included in the calculation, rather than just intrasexual conflicts (Males, *Mann-Whitney-Wilcoxon Test* $U = 916.5$, $n = 36$, $p = 0.003$; Females, $U = 879$, $n = 36$, $p = 0.009$, Figure 1B).

Accuracy of measures of intersexual dominance

The four measures of intersexual dominance differed in their accuracy [*Likelihood ratio test*: $X^2_{(3)} = 58.78$, $p < 0.0001$]. The Female Dominance Index and proportion of intersexual conflicts initiated correlated most strongly with internal values and correlated significantly more strongly than other measures (Figure 2A, Table 3). Nevertheless, values of all measures of intersexual dominance based on observed behavior significantly correlated with each other ($p < 0.0001$), and their correlation coefficients ranged from 0.74 to 0.91 (Figure 2B).

Measures of intersexual dominance were significantly less accurate when the intensity of aggression was low than medium or high and the degree of sexual dimorphism did not influence the accuracy of measures [Intensity of aggression: $X^2_{(2)} = 178.14$, $p < 0.0001$, emmeans *post-hoc*, High, Medium (sexual dimorphism), and Medium (monomorphism) intensity vs. Low intensity $p < 0.0001$, Supplementary Table S9]. Larger group sizes resulted in weaker accuracy in all four measures of intersexual dominance (Group Size: estimate $= -0.051$, SE $= 0.0038$, $p < 0.001$), while sex ratio did not have a significant effect (estimate $= -0.18$, SE $= 0.16$, $p = 0.28$) (Figure 2C).

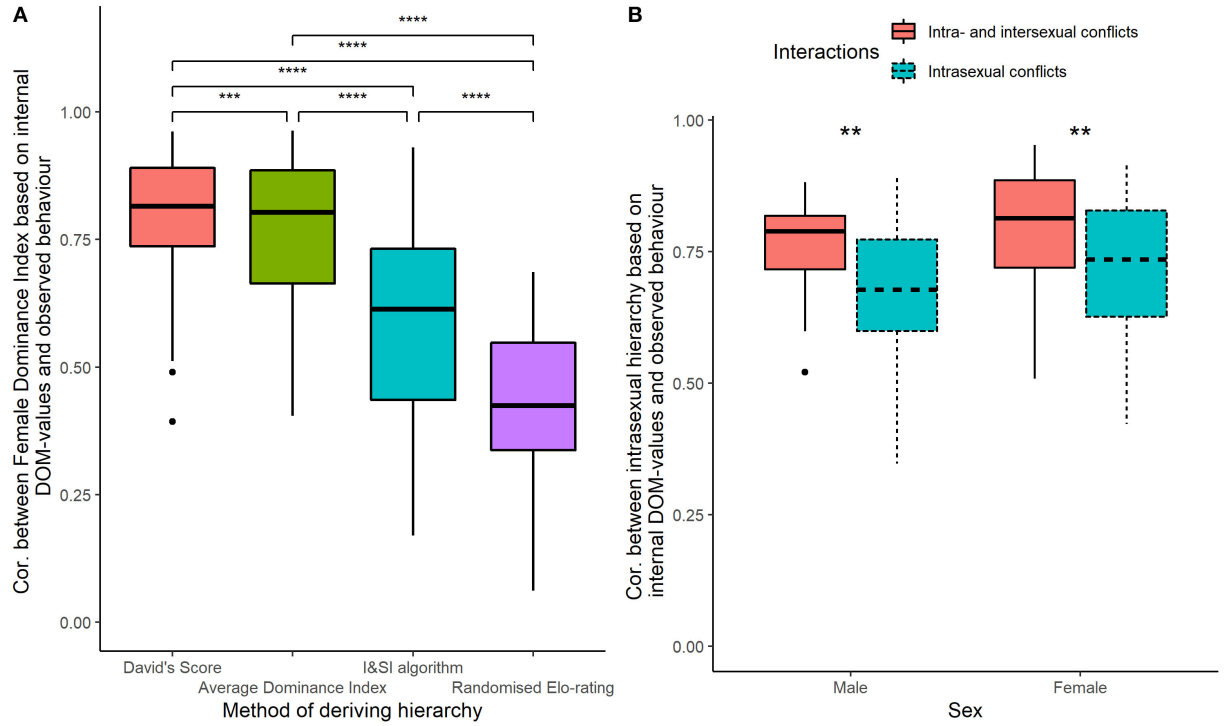

FIGURE 1
(A) Spearman correlation coefficient between the degree of intersexual dominance calculated using Female Dominance Index based on internal values and Female Dominance Index based on observed outcomes of dominance interactions for different methods of deriving a dominance hierarchy for 36 different parameter settings (40 runs per setting). **(B)** Spearman correlation coefficient between the intrasexual hierarchy based on internal DOM-values and the intrasexual hierarchy for each sex calculated from all conflicts of both sexes (intra- and intersexual conflicts) or intrasexual conflicts only. $^{**}p < 0.01$, $^{***}p < 0.001$, $^{****}p < 0.0001$.

Robustness of measures of intersexual dominance

We studied the influence of a higher proportion of missing data (and therefore a higher proportion of unknown relations, Supplementary Figure S4) on measures of intersexual dominance. Most measures indicated stronger dominance of females over males when more data were missing. In the case of the proportion of female-dominant dyads, missing data significantly increased female dominance in 94% of the parameter settings. This increase was true for 47% of the parameter settings of the Female Dominance Index, 53% of parameter settings for the proportion of intersexual conflicts won, and none of the parameter settings for the proportion of intersexual conflicts initiated (Figure 3, Supplementary Table S11).

Discussion

We studied in the model DomWorld (Hemelrijk, 1999) the accuracy (correlation with internal values) and robustness (influence of a reduced dataset) of four measures of intersexual dominance commonly used in the literature: the Female Dominance Index, the proportion of intersexual conflicts won, the proportion of intersexual conflicts initiated and the proportion of female dominant dyads. The Female Dominance Index and the proportion of intersexual conflicts initiated were more accurate than the other measures across a range of group sizes, intensities of aggression, and sex ratios. Regarding robustness, the proportion of intersexual conflicts initiated was the only measure that was robust to missing data. Nevertheless, all four measures performed well, and the degree of intersexual dominance was significantly correlated among them.

Female Dominance Index

The Female Dominance Index is the average proportion of males that rank below females in a dominance hierarchy of both sexes (Hemelrijk et al., 2008). Values of intersexual dominance based on Female Dominance Index were most accurate when using DS to calculate the dominance hierarchy, followed closely by the ADI while I&SI and randomized Elo-rating were the least accurate. These results support the conclusions from a former study that assessed the accuracy of dominance hierarchies in DomWorld and also showed that DS was slightly better than ADI and that I&SI performed worst (Hemelrijk et al., 2005). It

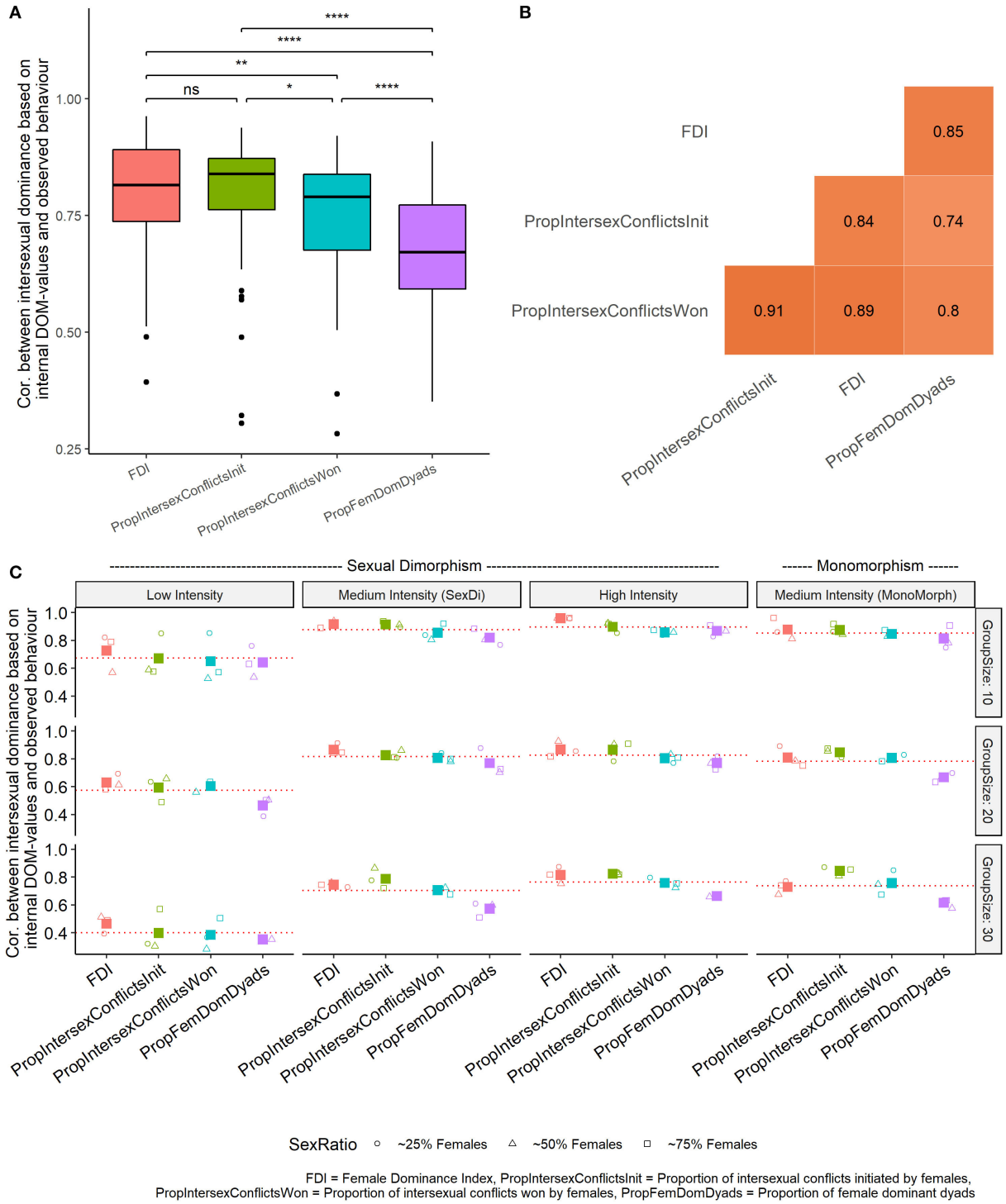

FIGURE 2
(A) Median and inter-quartile ranges of Spearman correlation coefficients of measures of intersexual dominance based on observed wins and losses and based on internal DOM-values (36 parameter settings, 40 runs per setting) for four ways of measuring intersexual dominance. *$p <$ 0.05, **$p < 0.01$, ****$p < 0.0001$. **(B)** Spearman correlation matrix among values from measures of intersexual dominance, based on all runs from all parameter settings combined ($n = 1{,}440$). **(C)** Spearman correlation coefficient between intersexual dominance based on measures using observed behavior and based on internal DOM-values in relation to the intensity of aggression and group size. Red dotted lines indicated the mean correlation coefficient for that parameter setting (based on all measures). Large solid squares indicate averages for all sex ratios for each measure of each combination of group size and intensity of aggression.

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TABLE 3 Emmeans *post-hoc* comparisons of the accuracy of different measures of intersexual dominance.

Comparison	Estimate	*SE*	*P*-value
Female Dominance Index—Proportion intersexual conflicts won by females	0.295	0.088	0.006
Female Dominance Index—Proportion intersexual conflicts initiated by females	0.038	0.090	0.974
Female Dominance Index—Proportion female dominant dyads	0.649	0.086	0.000
Proportion intersexual conflicts won by females—Proportion intersexual conflicts initiated by females	0.256	0.088	0.021
Proportion intersexual wins by females—Proportion female dominant dyads	0.354	0.084	0.000
Proportion intersexual conflicts initiated by females—Proportion female dominant dyads	0.610	0.086	0.000

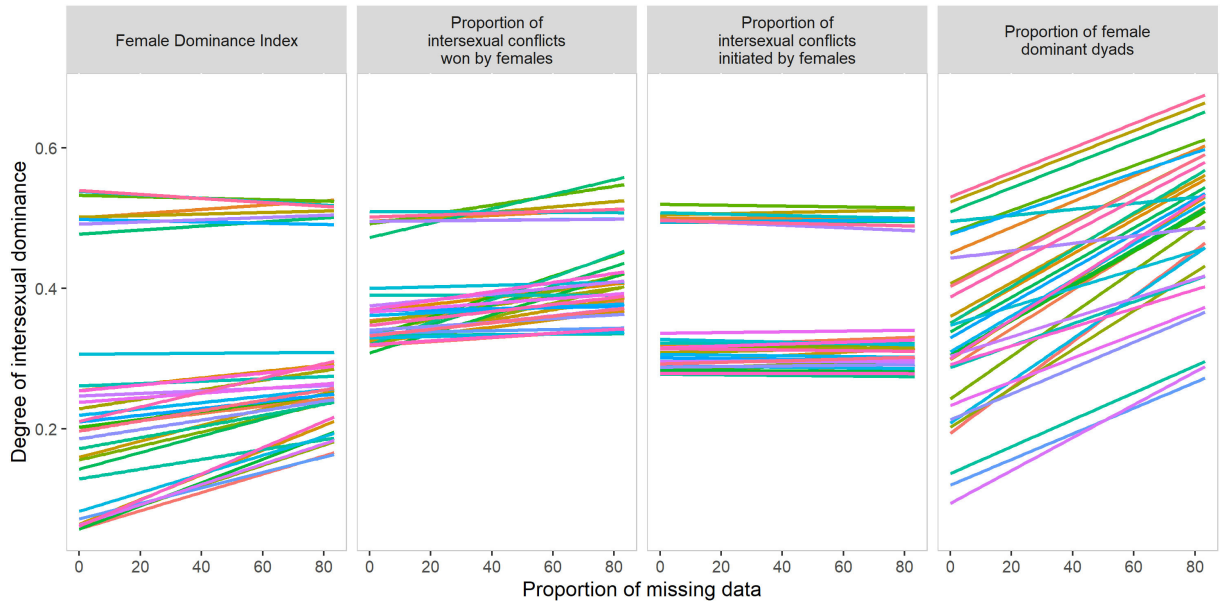

FIGURE 3
The relationship between measures of intersexual dominance and proportion of missing data for 36 parameter settings in DomWorld.

should be noted that the aim of I&SI is to produce a maximally linear dominance hierarchy which is neither always the case in hierarchies produced in DomWorld (de Vries, 2009), nor in real animals (Douglas et al., 2017). Thus, I&SI should only be used when a hierarchy can be assumed to be linear (de Vries, 1998).

In DomWorld, randomized Elo-rating did not produce a dominance hierarchy similar to that based on the internal dominance values and thus performed poorly compared to other measures. This result contradicts a study that demonstrated randomized Elo-rating is preferable to other methods for more egalitarian groups (Sánchez-Tójar et al., 2018). We attribute this disagreement to the different methods used. In the study of Sánchez-Tójar et al. (2018), interactions were simulated according to pre-assigned and static dominance ranks of individuals where the difference in winning probability between two adjacently ranked individuals was constant. Thus, patterns of interactions may have been less realistic than those in DomWorld where dominance is dynamic and reflects experience with victory and defeat with other group members and patterns of behavior have been shown to resemble those of real animals (Hemelrijk et al., 2017).

The Female Dominance Index and the proportion of intersexual conflicts initiated were the most accurate measures from those studied here (although the Female Dominance Index had a higher minimum, maximum and mean values than the proportion of intersexual conflicts initiated, Supplementary Table S6). We consider Female Dominance Index to be theoretically superior to other

methods since it incorporates both intrasexual (same-sex) and intersexual (between-sex) conflicts, both of which may influence an individual's propensity to win in its subsequent fight through the winner–loser effect. In DomWorld, intrasexual dominance hierarchies were more accurate when hierarchies were built using outcomes from conflicts among all adults as opposed to just intrasexual conflicts. In line with this, an empirical study has shown that the location of individuals in a hierarchy based on same-sex conflicts correlated strongly with their location in the hierarchy based on conflicts among all adults, suggesting the two hierarchies are highly related (Kappeler et al., 2022b). Thus, we propose that when studying intrasexual dominance, intersexual conflicts should also be considered because they may induce winner–loser effects which influence an individual's ability to win intrasexual conflicts, and their inclusion may make intrasexual hierarchies more accurate. Future studies should investigate how similar or different hierarchies built from same-sex conflicts are to those built from all conflicts among adults. Moreover, evidence that the winner–loser effect occurs in conflicts between the sexes is unclear and, thus, needs to be studied in the future.

Accuracy and robustness of different measures

Measures of intersexual dominance were more accurate when the group size was smaller and when the intensity of aggression was higher. In smaller groups in DomWorld, most individuals interact with each other (no unknown relationships) and when the intensity of aggression is higher the hierarchy is more differentiated and resembles a more despotic species (Hemelrijk, 1999). Thus, in real animals, measures of intersexual dominance may be more accurate when groups are smaller and when groups are more despotic because in both cases dominance relations are easier to infer. Interestingly, sexual dimorphism had no influence on the accuracy of measures of intersexual dominance. Therefore, the same measures of intersexual dominance are useful for different species, even if the sexes differ in their body size or intensity of aggression.

The Female Dominance Index and the proportion of intersexual conflicts initiated were significantly more accurate measures of intersexual dominance than the other two measures. Yet, the proportion of intersexual conflicts initiated was the only measure that was not influenced by missing data. A high proportion of unknown relationships has been shown to influence measures of intersexual dominance (Kappeler et al., 2022b). Here, we demonstrate that more unknown relations caused three of our four measures to overestimate the degree of female dominance over males. Thus, in the case of animals that do not interact frequently, the proportion of intersexual conflicts initiated might be more appropriate than Female Dominance Index to measure the degree of intersexual dominance.

When possible, we recommend reporting both the Female Dominance Index and the proportion of intersexual conflicts initiated in studies of intersexual dominance. These measures reflect different aspects of dominance between the sexes and reporting them together helps to distinguish between these aspects. The Female Dominance Index indicates where on average females are positioned in the hierarchy relative to males, while the proportion of conflicts initiated by females indicates how uni-directional the agonistic relationship between the sexes is. For example, in a group, some females may dominate some males according to the Female Dominance Index without females ever initiating conflicts against males (thus, the proportion of intersexual conflicts initiated equals zero). This is the case in some species of primate where females are dominant over some males because these males are attacked frequently by other males and fall in rank below some females (e.g., Hemelrijk et al., 2008). Moreover, sometimes females attack some males despite being lower in rank than these males (here, the Female Dominance Index may be zero, while the proportion of intersexual conflicts initiated is greater than zero).

Generalizability

In this study, we ignore the reasons why individuals engage in conflicts. We assume that this approach makes our results of general relevance. Moreover, although this study was not based on real animals, we replicated some results from an empirical study that compared measures of intersexual dominance (Kappeler et al., 2022b). Namely, values of intersexual dominance from the different measures were highly correlated with each other, indicating that all measures of intersexual dominance are equally useful. However, using DomWorld, we have shown more subtle differences among the measures because of our access to "real" internal dominance values and the large amount of data we can simulate. Nevertheless, our study has some limitations that may affect the generalizability of our conclusions to real animals. First, the internal degree of intersexual dominance was calculated using the Female Dominance Index based on internal DOM values which may have biased the internal values to correlate stronger with the Female Dominance Index (calculated with DS) more than the other measures. However, since all our measures were significantly correlated with each other as well as having similar levels of accuracy with internal values, we do not think there is a strong bias.

Second, in DomWorld an individual will initiate a fight if it thinks it will win, based on a ratio of its own and its partners' dominance values compared to a random number. This rule may not precisely reflect the real motivation of animals and

thus, individuals in DomWorld may have a higher (or lower) propensity to initiate fights that they do not win than in real animals. Indeed, in sifakas, there seems to be an interesting relationship between sex, initiation of agonistic interactions, and the ability to win. Under certain conditions, males were more likely to win intersexual conflicts if they initiated them than if they did not, despite intersexual dominance being biased toward females (Lewis et al., 2022). Thus, more research is required on why individuals initiate conflicts, especially in intersexual dyads, and whether the proportion of intersexual conflicts initiated reflects intersexual dominance relations well in real animals.

Conclusion

We studied the accuracy of four measures of intersexual dominance in a computational model, DomWorld, because its patterns of dominance resemble those in empirical data (Hemelrijk et al., 2017). We demonstrate that in smaller or more despotic groups, all four measures were more accurate. We urge future studies to report intersexual dominance by using two of our most effective measures together, the Female Dominance Index and the proportion of intersexual conflicts initiated. We highlight the need to include both intra- and intersexual conflicts when inferring a dominance hierarchy, even when considering dominance among members of a single sex.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: DataVerseNL: https://doi.org/10.34894/FX1R29.

Author contributions

LS, TS, and CH were involved in the conceptualization of the study. LS analyzed the data and drafted the manuscript. All authors contributed to discussions and editing of the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.982507/full#supplementary-material

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Male intrasexual aggression and partial dominance of females over males in vervet monkeys

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Females dominate a subset of the males in a minority of mammalian species despite male-biased sexual dimorphism. How this may arise is suggested by a computational model, DomWorld. The model represents male-biased sexual dimorphism through the males' greater initial dominance and higher intensity of aggression, meaning that fights initiated by males have a greater impact than those by females. The model shows that female dominance over males increases with a greater proportion of males in the group. This happens because when males are involved in a larger fraction of fights this results in greater hierarchical differentiation (i.e., steepness). This causes rank overlap between the sexes (i.e., partial female dominance). We test the validity of these processes in vervet monkeys (*Cercopithecus pygerythrus*), a primate species with partial female dominance. We confirm that the proportion of males in the group is significantly positively correlated with the degree of dominance by females over males and with the steepness of the hierarchy among males exclusively, but not with the steepness of the hierarchy among all adults of the group. The steepness in male hierarchies correlated positively with female dominance over males in these groups. We show that steeper hierarchies among vervet males resulted from male-to-male fights being a larger proportion of the fights among all adults of the group. We conclude that the higher frequency of male intrasexual aggression favors female dominance in vervet monkeys. We also show that females received coalitionary support when they were in conflict with a male, mainly from other females, and that this favors female dominance in this species, but this does not explain why partial female dominance increased with the proportion of males in the group. We advocate further investigation of the influence of male intrasexual aggression on the degree of female dominance over males in other species with partial female dominance.

KEYWORDS

female dominance over males, male intrasexual aggression, sexual competition, female coalitions, sex ratio

Introduction

Females are seldom dominant over males in competitive interactions in mammals (Holekamp and Engh, 2009). This is usually explained by males being larger than females and better armed (e.g., longer canines; Clutton-Brock, 2016), the prior attribute hypothesis (Chase et al., 2002). Indeed, in species in which females show complete dominance over males (e.g., spotted hyena, *Crocutta crocutta*: Tilson and Hamilton, 1984; several lemur species: Kappeler, 1993) sexual dimorphism is biased toward females (spotted hyena: Swanson et al., 2013), or non-significant (lemurs: Kappeler, 1990; rock hyrax, *Procavia capensis*: Koren et al., 2006). However, there are cases in which females—despite being smaller than males—show partial dominance over males (e.g., bonobos, *Pan paniscus*: Paoli et al., 2006; vervet monkeys, *Chlorocebus pygerythrus*: Struhskarer, 1967; Smuts, 1987; Hemelrijk et al., 2008; Young et al., 2017; capuchin monkeys, *Sapajus spp.*: Izar et al., 2021). The existence of 'partial female dominance' (Smuts, 1987) has been explained through social dynamics, such as coalitions of females against males (Smuts, 1987; White and Wood, 2007; Tokuyama and Furuichi, 2016), a reduction of aggression by males to females in exchange for sexual access named the docile male hypothesis (Surbeck and Hohmann, 2013), and frequent victimization of males by other males, so that they become low in rank *via* the self-reinforcing effects of winning and losing fights (the winner-loser effect), where a high intensity of aggression and a high proportion of males in the group lead to a larger degree of female dominance (Hemelrijk et al., 2008). The winner-loser effect implies that individuals are more likely to win a fight after winning a previous one, and vice versa for losing (Chase, 1982).

Female dominance over a subset of males was shown to emerge through the self-reinforcing effects of winning and losing fights in a computational model of dominance interactions in groups, based on self-organization, DomWorld (Hemelrijk, 1999). In the model, individuals start the simulation with an internal dominance value that determines their probability to win fights. Here, individuals with higher dominance values are more likely to win fights against individuals with lower dominance values. The winner-loser effect is reflected by the change in the dominance value of each individual after a fight, with the winner increasing its dominance value and the loser decreasing it. To reflect the sexual dimorphism of primates with males having a larger body size and better armament than females, males start in the simulation with a higher dominance value than females and their aggression is more intense. The initial dominance values of all individuals of the same sex are equal. The intensity of aggression influences the magnitude of the change of the dominance value of the two combatants after a fight. Fights started by a male result in greater change of dominance of both opponents than those started by a female, reflecting the higher intensity of aggression by males than females. We include more information about the equations underlying dominance interactions in DomWorld in the **Supplementary material**. In the model, partial female dominance over males develops despite females starting the simulation with lower dominance than males. It develops specifically when males were more intense in their aggression than females (the same pattern was not found for lower intensity of aggression by males), and more strongly the greater the proportion of males in the group (Hemelrijk et al., 2008). This happens because during the simulation, the dominance hierarchy of both sexes becomes steeper, i.e., the internal dominance values of each sex become more differentiated, when proportionally more males are present in the group, due to the higher intensity of aggression by males than females (Hemelrijk et al., 2008). Thus, in groups with a higher proportion of males, some males will drop down the hierarchy below some females because of the increased proportion of defeats from other males they have experienced, and some females will end up dominating some males without necessarily having ever fought against them (Hemelrijk et al., 2003). The winner-loser effect, on which the computational model is based, has been found across taxa (e.g., Hsu et al., 2009; Hirschenhauser et al., 2013; Kar et al., 2016), such as primates (Barchas and Menzosa, 1984; Eaton, 1984; Franz et al., 2015) including humans (Page and Coates, 2017). The self-reinforcing effect of winning or losing a single fight lasts up to 2 months in some species (Lan and Hsu, 2011).

So far, empirical support for the positive relationship between the degree of female dominance over males and the proportion of males in the group and has been found in (1) macaques; in a few groups of rhesus macaques, *Macaca mulatta,* and between several species of despotic macaques, *Macaca* spp. (Hemelrijk et al., 2008), (2) multiple groups of wild vervet monkeys (Hemelrijk et al., 2020), and (3) multiple groups of wild capuchin monkeys (Izar et al., 2021). Although these positive relationships support the predictions of the computational model DomWorld, we still need to investigate the dynamics proposed by the model to explain how this relationship arises in real life.

In line with the computational model DomWorld, we test whether (a) males are more intense in their aggression than females (necessary condition), (b) a larger proportion of males in the group leads to more fights in which males are involved (first prediction), (c) this leads to steeper hierarchies among all adults (second prediction), and (d) steeper hierarchies result in a larger proportion of males being subordinate to one or more females of high rank (i.e., partial female dominance, third prediction). We refer to this as the DomWorld Hypothesis.

Alternatively, a larger proportion of males in the group may result in stronger competition for mates among males due to the relatively lower availability of females. Therefore, males may become more intense in their aggression toward other males. Increased intra-sexual competition among males may result in a steeper hierarchy among males, but the steepness of the hierarchy among females would not be particularly influenced

by the increased male competition and thus the hierarchy among all adults would be less affected. A steeper hierarchy among males would imply that males are sinking in the hierarchy below an increasing proportion of females, increasing the degree of partial female dominance over males in a similar way as proposed by the computational model, DomWorld. We refer to these processes as the Male Competition Hypothesis.

We investigate these hypotheses in wild vervet monkeys in an enlarged dataset (with two more years of behavioral observations) compared to the one used by Hemelrijk et al. (2020) where they showed that the degree of female dominance increased with the proportion of males in the group. Our dataset consists of 22 group-year data points (from four groups of vervet monkeys). Vervet monkeys are an ideal study species because they meet the requirements underlying the DomWorld hypothesis (Hemelrijk et al., 2020; Izar et al., 2021) by showing partial female dominance over males (Hemelrijk et al., 2020), male-biased sexual dimorphism (Turner et al., 2018), intense aggression (Cheney and Seyfarth, 1990), and a large range of sex ratios, due to frequent male dispersal between groups and years (Cheney and Seyfarth, 1990).

Furthermore, we explore the role of coalitions between females against males in causing the partial female dominance in wild vervet monkeys. They are thought to maintain partial dominance of females over males in bonobos, regardless of the species' male-biased sexual dimorphism (Parish, 1996; Tokuyama and Furuichi, 2016) and help females win fights against larger males in several other species with male-biased sexual dimorphism, including vervet monkeys (reviewed in Smuts and Smuts, 1993). In vervet monkeys, Hemelrijk et al. (2020) showed that the proportion of intersexual fights in which a female received support from another female increased with the proportion of males in the group. This was considered to be a side effect of the higher rank of females in the group (thus lowering their risk when attacking) and was not considered as a potential reason why females are high ranking (Hemelrijk et al., 2020). Here, however, we argue that once females occupy higher positions in the hierarchy, female coalitions against males may further increase partial female dominance over males in those groups. Thus, a stronger tendency for females to form coalitions with other females against males in groups with proportionally more males may help explain why female dominance is higher in these groups. We refer to this hypothesis as the Female Coalition Hypothesis.

Materials and methods

Study species

In vervet monkeys, the sexes are dimorphic with males on average 1.4 times the weight of females (Turner et al., 2018), more muscular, and with canines on average 1.3 times the length of those of females (Bolter and Zihlman, 2003). Males disperse from the natal group when they reach sexual maturity (around 4 to 5 years-old), and subsequently disperse multiple times in their lifespan (Cheney and Seyfarth, 1990). In the new group they fight to establish their place in the dominance hierarchy (Cheney and Seyfarth, 1990). Females are philopatric and inherit their rank based on the rank of their mother (i.e., matrilineal society, Cheney and Seyfarth, 1990).

Data collection

Data were collected at the Inkawu Vervet Project (IVP) in the Mawana Game Reserve, South Africa, on four neighboring groups of wild vervet monkeys, named Ankhase, Baie Dankie, Kubu, and Noha. There is heterogeneity of vegetation both within the home range of each single group and between different groups, from areas of dense vegetation to areas with more sparse vegetation dominated by *Acacia* species. Data of social interactions were collected by *ad libitum* sampling (Altmann, 1974) from January 2011 to December 2019, after monkeys were habituated to human presence in ten meters vicinity in 2010. Researchers at the IVP are trained in collecting behavioral data and are required to pass a test for identifying all the monkeys they are collecting data on, as well as to perform periodical inter-observer tests ensuring that data collection is standardized among all researchers. Males were considered adult after emigrating from their natal group for the first time, and females after giving birth to their first offspring.

Data analyses

Competitive interactions

In our analyses we focused on adults. For being included in the analysis, individuals of both sexes had to be present in the group as adults for at least 6 months per year. For the DomWorld Hypothesis and the Male Competition Hypothesis, the analyses included only dyadic interactions, excluding interactions with support from a third party. For the Coalitionary Support Hypothesis, we also included agonistic interactions between adults receiving support from a juvenile or an adult. Regardless of the duration and complexity of the interaction, and regardless of eventual support from third parties, the individual that showed as its last behavior an act that was clearly aggressive ("stare," "attack," "grab," "displacement," "bite," "hit," "chase," "aggressive call," "steal food," and "hand on head") was noted as the winner and the individual showing a clearly submissive behavior as the loser of the interaction ("avoid," "jump," "crawl," "leave," "retreat," "flee," and "scream") (Hemelrijk et al., 2020). In the following cases, the interactions were not used because they were not unequivocally defined. (1) An individual spontaneously showed submission to another

or there was no reaction from the victim to an (attempted) aggression. (2) One or both individuals displayed a last behavior that was not clearly submissive or aggressive (e.g., "undetermined vocalization"). (3) The last behavior of both individuals was similar—both were aggressive or submissive. Note that supporters involved in triadic interactions to help one of the two opponents were not counted as winning or losing interactions.

Following these criteria, we analyzed 4578 dyadic interactions from 123 distinct individuals—69 females and 54 males—from four groups, over a period of up to 9 years, with a total of 22 group—year points (**Table 1**). The average number of adults per group was 14.7 (standard deviation = 6.8), number of adults per group ranged from six to 32 individuals, and group size varied between years (**Table 1**). Females were usually the most abundant sex, with an average proportion of males in the group of 0.31 (standard deviation = 0.12); the group with the smallest proportion of males was Noha in 2011, with one male and nine females (0.10), while the one with the largest proportion was Baie Dankie in 2014, with eight males and seven females (0.53).

Intensity of aggression

For the intensity of aggression, we classified interactions with physical contact (hit, bite, chase, grab, steal food, or hand on head) as severe and interactions without (stare, displace, and aggressive call) as mild. For each aggressive interaction, we considered only the initiator to be responsible for the intensity of the aggression. If an individual reacted with a severe aggressive behavior after receiving severe aggression, its behavior was not counted as being severe aggression, since it was responding to severe aggression received from another individual instead of causing it. Also, if an individual escalated a mild interaction with a severe behavior, it was counted as showing severe aggression even though it did not initiate the interaction.

We measured the intensity of aggression in two ways. (1) The average proportion of severe fights of the total number of fights per individual, and (2) the average absolute number of severe fights per individual. We used both metrics to compare the intensity of aggression of males to females in each group-year point.

We investigated the intrasexual competition among males by two metrics. The first concerned intensity of competition, namely the proportion of intrasexual severe fights by males of all severe aggressive acts by males against adults. This metric quantified which part of their intense aggression males directed to other males, thus controlling for any differences in the frequency of aggression per year related to socioecological factors. The second metric concerned the relative frequency of competition among males from that among all adults (ignoring its intensity), namely the proportion of male-to-male fights of all group fights among adults. This metric quantified how often male-to-male aggression occurred in a group during each year, controlling for different baseline frequencies of aggression among adults that may differ among groups and years due to socioecological variables.

The dominance hierarchy, female dominance, and hierarchical steepness

To determine the dominance hierarchy among adults, we organized competitive interactions in matrices with the winners in the rows and losers in columns. Interaction matrices were calculated per group and per year, excluding group-year points with less than 50 dyadic competitive interactions, as done by Hemelrijk et al. (2020). We calculated the rank of each individual by the average dominance index, ADI (Hemelrijk et al., 2005). It is the average proportion of winning by an individual from all its group members excluding those with whom it did not interact competitively.

We quantified the degree of female dominance in each group-year point by the Female Dominance Index (Hemelrijk et al., 2008). Here, we make use of both intrasexual and intersexual aggressive interactions. The Female Dominance Index represents the proportion of males that each female is dominant over, averaged over all females in the group; this value ranges from 0 (complete male dominance; i.e., zero female dominance over males) to 1 (complete female dominance; i.e., all females are dominant over all males). If a female and a male are equally dominant, the male is counted as being co-dominant in the calculation of the Female Dominance Index by contributing half a unit (0.5).

We calculated the steepness of the hierarchy as the slope of the linear regression between the ordinal rank of the individuals and the dominance index of each individual (de Vries et al., 2006). Because unknown relationships were present in the interaction matrices of our dataset and the steepness measure based on the normalized David's score is strongly biased by this (Klass and Cords, 2011), we based the steepness measure on the normalized average dominance index instead, as it was less affected by unknown relationships (Saccà et al., 2022). We measured the hierarchical steepness, and investigated the effect for both all adults of the group and for exclusively the adult males among all adults of the group (i.e., the male sub-hierarchy). In the male sub-hierarchy, each male kept his dominance index (thus his relative rank) as calculated for the hierarchy of all adults. We used these values of the dominance indices instead of the dominance indices derived from competitive interactions among males only, in order to account for the influence *via* the winner-loser effect that all fights (intersexual fights, as well as fights among males and among females) have on males' cardinal and ordinal ranks. Thus, we test the hierarchical differentiation (i.e., steepness) among males including the dynamics of interaction among all adults. It should be noted that in multiple species (among which vervet monkeys) the rank order of same sex individuals was highly correlated between dominance hierarchies based on

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TABLE 1 Information on groups per year (in parentheses) regarding the number (#) of adults of each sex, the proportion of males, the number of dyadic fights, the degree of female dominance (i.e., Female Dominance Index) from dyadic interactions and when interactions with support were added to the calculation of the dominance hierarchy, and the steepness of the hierarchy of all adults and of males only.

Group*[1] (Year)	# of males	# of females	Proportion of males	# of dyadic fights	FDI (dyadic fights)	FDI (with support)	Steepness of hierarchy (male subset)	Steepness of hierarchy (all adults)
AK (2011)	2	5	0.29	144	0.00	0.00	0.15	0.87
AK (2012)	6	6	0.50	70	0.58	0.63	0.99	0.96
AK (2013)	4	9	0.31	66	0.51	0.61	0.78	0.88
AK (2019)	1	7	0.13	80	0.29	0.43	NA*[2]	0.78
BD (2011)	4	8	0.33	478	0.25	0.28	0.88	1.04
BD (2012)	4	12	0.25	171	0.46	0.50	0.57	0.74
BD (2013)	4	11	0.27	58	0.43	0.50	0.71	0.92
BD (2014)	8	7	0.53	54	0.42	0.42	0.95	1.05
BD (2015)	6	11	0.35	95	0.38	0.49	0.84	0.95
BD (2016)	6	11	0.35	116	0.27	0.30	0.77	0.92
BD (2017)	12	12	0.50	527	0.40	0.53	0.73	0.83
BD (2018)	13	16	0.45	501	0.41	0.44	0.85	1.01
BD (2019)	12	20	0.38	407	0.36	0.48	0.61	0.76
KB (2017)	1	5	0.17	83	0.00	0.00	NA*[2]	0.97
KB (2019)	1	5	0.17	57	0.00	0.00	NA*[2]	0.95
NH (2011)	1	9	0.10	764	0.00	0.00	NA*[2]	0.93
NH (2012)	5	10	0.33	150	0.52	0.67	0.74	0.93
NH (2013)	5	11	0.31	151	0.45	0.47	0.76	0.98
NH (2014)	7	11	0.39	80	0.27	0.32	0.67	0.96
NH (2016)	2	6	0.25	118	0.08	0.17	0.11	0.85
NH (2018)	3	9	0.25	150	0.50	0.55	0.85	0.91
NH (2019)	3	12	0.20	258	0.33	0.36	0.52	1.00

[1] Abbreviations of group names are AK, Ankhase; BD, Baie Dankie; KB, Kubu; NH, Noha. NA[2]: Steepness of sub-hierarchy among males could not be calculated for groups with 1 male.

interactions among the same sex only and on among both sexes (Kappeler et al., 2022). When only a single male was present in a group, it was impossible to calculate the steepness of the hierarchy among males and therefore, this group-year point was excluded from the analyses (so, four group-year points were excluded).

Statistics

We analyzed the relation between the degree of female dominance over males and the proportion of males in our enlarged dataset, in which we added 2 years of observation for the four groups in the Mawana reserve to the data used by Hemelrijk et al. (2020). We did this because this relation is essential to our analyses, and although the relation was shown by Hemelrijk et al. (2020) to be positive and significant it needed confirmation with our updated and enlarged dataset. We used a Generalized Linear Mixed Model (GLMM from now on) assuming a beta-binomial distribution of the response variable, the Female Dominance Index, similarly to Hemelrijk et al. (2020), with the proportion of males in the group as the explanatory variable and with the group of each group-year point as the random part of our model. We tried to fit a GLMM adding also the effect of the years to the random part of the model, but we could not because this led to problems in model convergence.

We investigated whether the steepness of the hierarchy, either among all adults or the subset of males only from the hierarchy among all adults (the male sub-hierarchy), can explain the aforementioned relationship as it was proposed by the DomWorld Hypothesis or by the Male Competition Hypothesis. We tested our hypotheses by analyzing the relationships between three variables: the proportion of males in the group, the hierarchical steepness (of either all adults or the subset of males), and the degree of female dominance over males (Female Dominance Index).

The DomWorld hypothesis

To investigate the DomWorld Hypothesis, we investigated the relation between the hierarchical steepness among all adults and the proportion of males in the group. In the DomWorld Hypothesis, this relation is expected to be positive and significant. We tested this in a Linear Mixed Model (LMM

from now on), with the hierarchical steepness as the response variable and the group and year of each group-year point as random effects. We assumed a Gaussian distribution for the hierarchical steepness because the steepness of the group can reach values over one, which is a characteristic of the steepness measure when it is calculated for interaction matrices in which not all relationships are known (Saccà et al., 2022). Next, we tested whether the Female Dominance Index was related to the steepness of hierarchy among adults. We expect this relationships to be positive and significant, if the hypothesis is correct. Here, we used a GLMM assuming a beta-binomial distribution of the response variable, the Female Dominance Index, with the steepness of hierarchy among adults as the explanatory variable and the group of each group-year point as the random part. We could not include the year as a random effect because of problems in model convergence.

We investigated whether males and females differ in the intensity of aggression, since the DomWorld Hypothesis assumes that males are more intense in their aggression than females. For this we compared two metrics of intensity of aggression: the average proportion of severe fights of the total number of fights per individual and the average number of severely aggressive interactions per individual. We compared these two measures between the sexes for each group-year point using a non-parametric test, namely the Wilcoxon signed-rank test, because the distribution of the differences between the values of males and those of females for both metrics of intensity of aggression was not normal (based on the Shapiro-Wilk test for normality).

When examining the relation between the proportion of fights with males (of all fights among adults) with the proportion of males in the group, we used a GLMM assuming a beta-binomial distribution of the response variable, the proportion of fights with males (of fights among all adults), and the year and group of each group-year point as the random part. We expect that the proportion of fights with males increases with the proportion of males. When testing whether the proportion of male fights is related with the steepness of the group hierarchy, we used a LMM with the steepness of the hierarchy among adults as the response variable, and the random effects for the years and groups of each group-year point, and according to the DomWorld Hypothesis we expect the steepness to increase with the proportion of males.

The male competition hypothesis

In the Male Competition Hypothesis, we tested the relation between the steepness of the male sub-hierarchy, namely the hierarchy among males (when males were interacting with all adult group members) with the proportion of males in the group. According to the Male Competition Hypothesis, we expect the steepness of males to increase with the proportion of males in the group. Here, we used a LMM, with the steepness of the sub-hierarchy among males in the group as our response variable, and with the random part of the model composed of the effect of group and year for each group-year point. We assumed a Gaussian distribution because the steepness could theoretically reach values higher than one. Next, we tested the relation between the Female Dominance Index and the steepness of hierarchy in the subset of males using a GLMM assuming a beta-binomial distribution of the response variable, the Female Dominance Index. In line with the Male Competition Hypothesis, we expect female dominance over males to increase with increased steepness of the male sub-hierarchy.

We tested whether greater steepness of the hierarchy among males with a larger proportion of males may be due to an increase of intrasexual competition among males *via* more intense or frequent aggression among males. Thus we investigated the relation between the intensity and the frequency of male intrasexual aggression with the proportion of males in the group by using two GLMMs for two metrics of male intrasexual competition (intensity and frequency). We also investigated with two GLMMs the relation between the steepness of male sub-hierarchy and either intensity or frequency of male intrasexual competition.

In one GLMM we assumed a beta-binomial distribution for the proportion of male-to-male severe fights of all male severe fights (indicating the intensity of male intrasexual competition) and the proportion of males in the group was the explanatory variable, with the random part of the model formed by the year of each group-year point. We tried to fit a model with also the random effect of group, but we found that our fitted model showed significant quantile deviations in the plot of the residuals versus predicted values (DHARMa package for R: Hartig, 2022). In the other GLMM we assumed a Gaussian distribution for the hierarchical steepness among the subset of males separately (the male sub-hierarchy), with the proportion of male-to-male severe fights of all severe fights by males as the explanatory variable and the group and year of each group-year point as random factors.

Similarly, in another GLMM we assumed a beta-binomial distribution for the proportion of male-to-male fights of all fights among adults (i.e., representing male intrasexual competition), and using the proportion of males in the group as the explanatory variable, and the effects of group and year as the random part of the model. In the other LMM we assume a Gaussian distribution for the hierarchical steepness of the subset of males, and the proportion of male-to-male fights of all fights among adults was the explanatory variable, with the random part of the models being the effects of group and year for each group-year point.

When analyzing the Male Competition Hypothesis, we used group-year points with at least two males.

The female coalition hypothesis

To test the Female Coalition Hypothesis, we investigated whether the Female Dominance Index calculated for the

dataset including support in fights differed from the one without support in fights. We calculated the difference between the Female Dominance Index per group-year point when coalitionary support is included minus when it is excluded. A positive value means that partial female dominance increased in the group-year point when including support versus when not. We investigated whether the average difference differed from zero with a LMM with the difference in FDI values between group-years with and without coalitionary support as the response variable, no explanatory variable and the random effects of groups and years for each group-year point. The value and significance of the intercept of this model represent the difference between groups in female dominance over males when support is added. We did so to include the random effects of group and year for each group-year point in the analyses. We also investigated whether coalitionary support caused a larger degree of female dominance with an increasing proportion of males in the group than without coalitionary support. In our LMM, we assumed a Gaussian distribution for the difference in the values of the FDI between group-year points with and without coalitionary support as the response variable, and the proportion of males in the group as the explanatory variable and the random effects of group and year.

Information on statistical software, model diagnostics and model performance

All analyses were conducted in R, version 4.2.0 (R Core Team, 2022). To fit all our Generalized Linear Mixed Model and Linear Mixed Models we used the package glmmTMB (Brooks et al., 2017). For model diagnostics, in our **Supplementary material**, we show QQ-plots and plots of fitted residuals versus predicted residuals with relevant statistical analyses, obtained from the package DHARMa (Hartig, 2022). For model performance statistics, we calculate pseudo R2 values using the package MuMIn (Bartoń, 2022) and we perform likelihood ratio tests (LRT) comparing our full models to the same models without the explanatory variable, to test whether the change in likelihood was significant. For the LRT as well as for the Wilcoxon signed-rank tests and the Shapiro-Wilk tests we used the base package of R. Figures were made using the package ggplot2 (Wickham, 2016).

Results

The degree of female dominance over males, the Female Dominance Index, increased significantly with the proportion of males in the group (GLMM, 22 group-year points, $\beta = 2.41$, SE = 1.20, $P = 0.044$, **Figure 1A**) in line with earlier results from Hemelrijk et al. (2020) on a smaller dataset. To detect the processes underlying this relationship we study three hypotheses, the DomWorld Hypothesis, the Male Competition Hypothesis, and the Female Coalition Hypothesis.

The DomWorld hypothesis

The steepness of the hierarchy among all adults did not increase significantly with the proportion of males (LMM, 22 group-year points, Slope = 0.17, SE = 0.15, $P = 0.255$) nor with the Female Dominance Index (GLMM, 22 group-year points, $\beta = -0.19$, SE = 1.19, $P = 0.871$). Therefore, the steepness of the hierarchy among all adults did not explain the larger degree of female dominance in the group-years when the proportion of males in the group increased.

Although the proportion of fights with males of all fights among adults increased significantly when the proportion of males increased (GLMM, 22 group-year points, $\beta = 4.40$, SE = 1.01, $P < 0.001$), the increased proportion of fights among males was not related to the hierarchical steepness among adults (LMM, 22 group-year points, slope = 0.05, SE = 0.11, $P = 0.649$). This led to the question of whether the assumption was met that males were more intense in their aggression than females.

Although there was a trend that the average proportion of severe fights of all fights by males was higher than that by females, it was not significant (Wilcoxon signed-rank: 22 group-year points, $V = 184$, $P = 0.063$, **Supplementary Figure 1**, median: 9.0% for males versus 7.4% for females). Neither did males and females differ significantly in their average number of severe interactions per individual (Wilcoxon signed-rank test: 22 group year points, $V = 131$, $P = 0.602$, **Supplementary Figure 1**, median: 2.2 for males versus 1.8 for females).

The male competition hypothesis

The Female Dominance Index increased significantly with the steepness of the sub-hierarchy among males (GLMM, 18 group-year points with at least two males, $\beta = 1.69$, SE = 0.59, $P = 0.004$, **Figure 1D**) and the steepness of male sub-hierarchy increased significantly with the proportion of males in the group (LMM, 18 group-years with at least two males, slope = 1.36, SE = 0.49, $P = 0.005$). Therefore, the degree of female dominance may increase with the proportion of males in the group *via* the increased steepness of the male sub-hierarchy.

Both intensity and frequency of intrasexual aggression among males may lead to the increase in steepness of hierarchy in the subset of males. Concerning the intensity of male intrasexual aggression, males did not direct a significantly larger proportion of their intensely aggressive actions to other males when the proportion of males in the group increased (GLMM, 18 group-year points with at least two males, $\beta = 3.54$, SE = 2.03, $P = 0.081$), and the proportion of male-to-male

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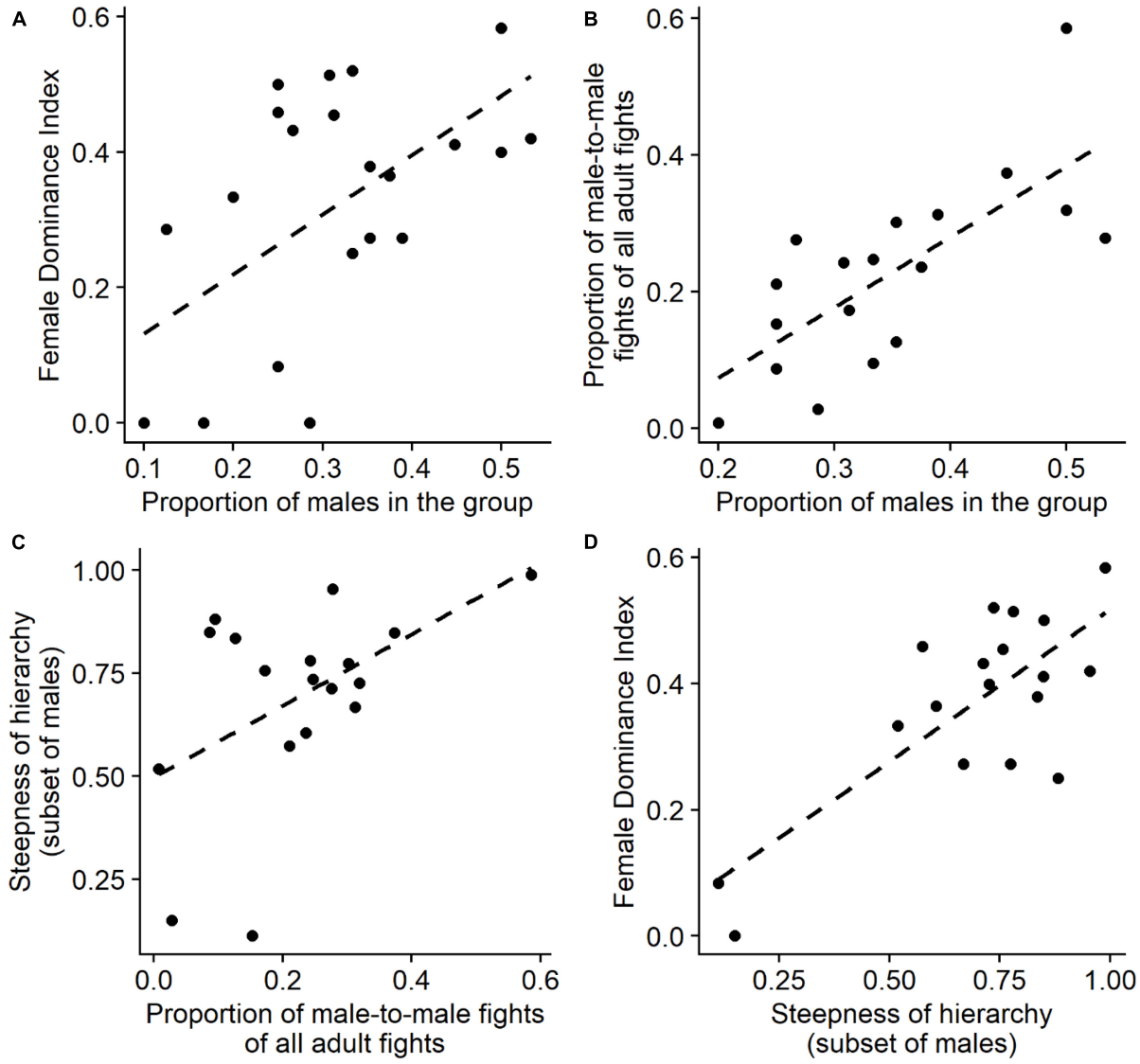

FIGURE 1
Summary of relevant relations for the Male Competition Hypothesis: **(A)** proportion of males in the group versus degree of female dominance (i.e., female dominance index, FDI) (22 group-year points). **(B)** The proportion of male-to-male fights of all adult fights (relative frequency of male intrasexual competition) versus the proportion of males in the group. **(C)** The steepness of hierarchy among the subset of adult males versus the proportion of male-to-male fights of all adult fights (i.e., relative frequency of male intrasexual competition). **(D)** The degree of female dominance (i.e., FDI) versus the steepness of hierarchy among the subset of adult males. Plots **(B–D)** concern only group-year points with at least two males (18 group-year points). Trend lines (dotted lines) are calculated for (ordinary least squares) linear regressions, using the function "geom_smooth" of the R package "ggplot2" (Wickham, 2016). For more accurate statistical analyses, see text.

severely aggressive interactions was not significantly related to the steepness of male hierarchy (LMM, 18 group-year points with at least two males, slope = 0.38, SE = 0.20, $P = 0.061$).

Concerning the relative frequency of male intrasexual aggression, a larger proportion of fights among adults were between males when the proportion of males in the group increased (GLMM, 18 group-year points with at least two males, $\beta = 6.82$, SE = 1.44, $P < 0.001$, Figure 1B), and a larger proportion of male-to-male fights was positively related to hierarchical steepness when studying the subset of males among the adults (LMM, 18 group-year points with at least two males, $\beta = 0.67$, SE = 0.35, $P = 0.014$, Figure 1C).

The female coalition hypothesis

Considering fights between a male and a female in which one or more external individuals intervened (there were 265 intersexual fights with support), support was overwhelmingly given to females (239 times, 90% of cases). In the intersexual

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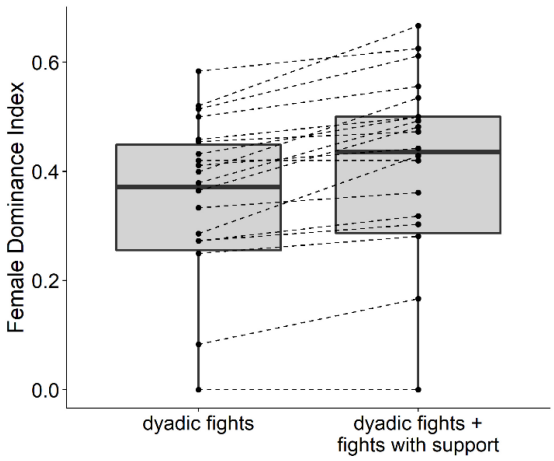

FIGURE 2
The Female Dominance index of the dominance hierarchy calculated from only dyadic fights **(left)** versus the hierarchy with the inclusion of fights with support **(right)**. Note that support was seldom received from more than one individual (23 cases from 239 cases; from two or more females in 5 cases, from two or more males in 8 cases, and from two or more individuals of both sexes in 6 cases, in 2 cases, support was received from a coalition of a female and unidentified juveniles, and in 2 cases from a coalition of a male and unidentified juveniles). In 26 cases in which a female received support in an intersexual fight the sex of the supporter could not be identified.

fights in which the female received support, this was provided mostly by a single adult female (111 times out of 239, 44% of cases), and less often by a single adult male (79 times, 33% of cases).

The degree of female dominance over males, the Female Dominance Index (FDI), increased significantly when including support in fights versus when not and considering the random effects of group and year (LMM, 22 group-year points, intercept = 0.056, SE = 0.010, $P < 0.001$, Figure 2). Results did not change when calculating the average difference in FDI irrespectively of random effects, likely because they had very little effect. Namely, on average per group-year point FDI increase by 0.056 (SE = 0.010), with a minimum of 0 and a maximum of 0.15. In all group-year points, female dominance was equal or higher when including fights with support. However, the difference between female dominance values when including fights with support or not was not significantly greater the higher the proportion of males in the group (LMM, 22 group-year points, slope = −0.06, SE = 0.09, $P = 0.515$).

Discussion

We confirm that the degree of female dominance over males increases with the proportion of males in four groups of wild vervet monkeys, in line with earlier findings by Hemelrijk et al. (2020). We found neither evidence that the steepness of the hierarchy among adults increased with the proportion of males in the group, nor that the degree of female dominance over males increased with the steepness of the hierarchy among adults, despite being suggested by DomWorld (DomWorld Hypothesis, see Figure 3). A requirement for the DomWorld hypothesis is that males are more intense in their aggression than females. However, we did not find evidence for this in vervet monkeys when we categorize severe aggression as fights with physical contact. Thus, this requirement of the computational model may be missing, which may explain that the predictions of the DomWorld Hypothesis were not met. However, it should be noted that male vervets are larger and better armed than females, thus making their fights with physical contact more menacing by default. Consequently, even without physical contact their attacks are probably perceived as more severe than those by females due to the threat of escalating the conflict.

Instead, the steepness of the hierarchy of the subset of males increased significantly with the proportion of males in the group and it was positively related to the degree of female dominance over males. This is in line with the Male Competition Hypothesis and may explain the higher degree of female dominance in group-year points with proportionally more males as being due to more males dropping down the hierarchy below a larger proportion of females. The steeper male hierarchy within the hierarchy of all adults, when the proportion of males in the group increased, may be due to an increase in frequency of male intrasexual conflicts, and was not related to an increase in the intensity of male intrasexual fights (Male Competition Hypothesis, see Figure 3).

The Male Competition Hypothesis resembles the DomWorld Hypothesis, because the self-organization processes underlying both hypotheses are similar. In the DomWorld Hypothesis males sink down the hierarchy below more females because the intensity of fights initiated by males is higher than initiated by females, and a higher proportion of males in the group results in more fights initiated by males and thus a steeper hierarchy for the whole group. In vervet monkeys, males probably sink down the hierarchy below more females because males fight more frequently among themselves the higher the proportion of males in the group, and thus the male hierarchy becomes steeper. In the model, a higher number of male-male fights when the group comprises more males would be expected from a simple self-organization process where more males being present in the group results in more male-male encounters by chance and thus, potentially, more fights among males. The same self-organization process could be expected in groups of wild primates. In vervet monkeys, the same increase in male-male fights with the proportion of males in the group may also reflect mating competition, as the presence of more males limits the access to females. The self-organization process and low availability of females

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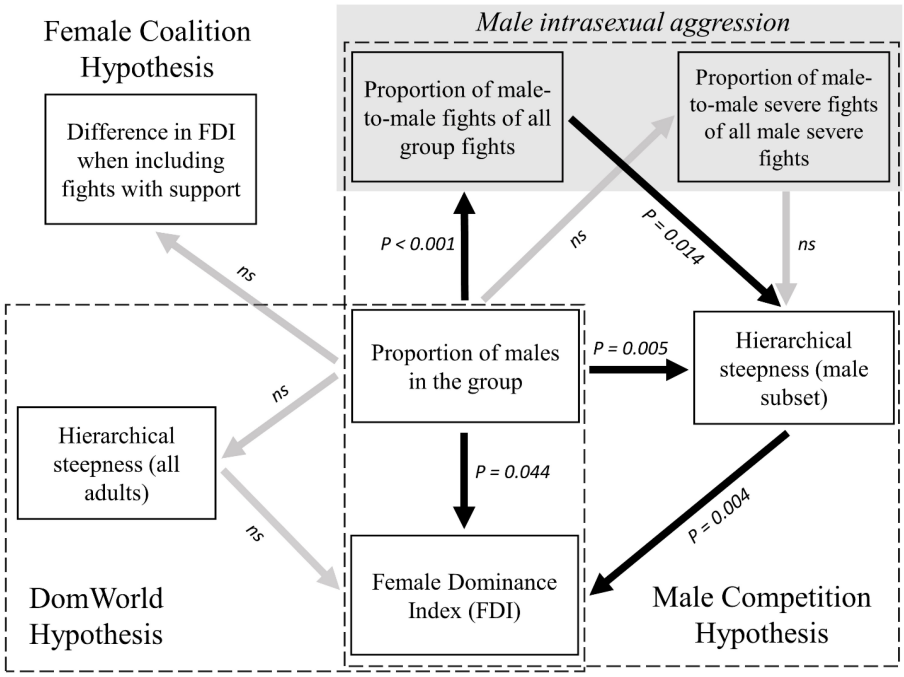

FIGURE 3
Summary of correlations related to the degree of female dominance (i.e., Female Dominance Index, FDI) in vervet monkeys. Correlations are represented as arrows pointing from the response variable to the explanatory variable. The statistical significance of each correlation is noted next to the arrow (with not significant values noted as *ns*). Significant correlations are noted as black arrows, while non-significant correlations as gray arrows. All significant correlations are positive.

can favor competition among males in a synergistic way. The self-organization processes underlying the Male Competition Hypothesis and the DomWorld Hypothesis differ in the absence of the requirement that males are more intense than females in their aggression in the Male Competition Hypothesis. Thus, the Male Competition Hypothesis can be relevant even in species in which sexual dimorphism is absent (e.g., lemurs: Kappeler, 1990) or in favor of females (e.g., spotted hyena: Swanson et al., 2013), where we do not expect males to be more intense in their aggression than females.

The similarities between the DomWorld Hypothesis and the Male Competition Hypothesis can be illustrated by the work by Izar et al. (2021). The study shows that in three study species of capuchin monkeys (*Sapajus libidinosus*, *S. nigritus*, and *S. xanthosternos*) not only did the Female Dominance Index increase with the proportion of males in the group, but so did the proportion of male-male aggression of total male aggression (Izar et al., 2021). However, Izar and colleagues did not distinguish between the effect that male fights have on the hierarchy of all adults (our DomWorld Hypothesis) and on the adult male sub-hierarchy (our Male Competition Hypothesis). If males are more intense in their aggression than females, an increase in male-male aggression (and thus in the steepness of male sub-hierarchies, the Male Competition Hypothesis) may still happen in combination with a larger proportion of male fights of all group fights (and thus in steeper hierarchies for the whole group, the DomWorld Hypothesis). Consequently, these two hypotheses are not mutually exclusive, and whether they happen jointly or independently probably depends on the characteristics of the species, and warrants further investigation.

Although coalitionary support by females to other females in fights between the sexes enhanced partial female dominance in vervet monkeys (**Figure 2** and **Table 1**), female dominance did not increase more when females received more support when the proportion of males in the group was larger (Female Coalition Hypothesis, see **Figure 3**). Therefore, coalitions by females did not cause the increase in female dominance with the increased proportion of males in the group (Female Coalition Hypothesis). These coalitions may instead be a by-product of the already higher status that females enjoy in groups with a larger proportion of males, as proposed by Hemelrijk et al. (2020). Males provided support to females in one third of intersexual conflicts in which a female received support from a third party. Females may recruit males with incentives to helpful males and disincentives to un-cooperative ones, as they do in intergroup fights (Arseneau-Robar et al., 2016b; or males may help females in exchange for increased mating success, as also observed in the context of intergroup encounters (Arseneau et al., 2015; Arseneau-Robar et al., 2016a).

In conclusion, our study of vervet monkeys partially supports the self-organization processes from DomWorld, as we give evidence that male intrasexual competition increases with the proportion of males in the group and favors partial female dominance in a way that could be explained by self-organization processes also present in the computational model. The increase in male-male competition when the proportion of males in the group increases could be due to self-organization processes, to male competition due to lower female availability, or a combination of self-organization and male competition, and may be a widespread phenomenon in group-living animals. Future studies should try to disentangle the effect that the self-organization process and mating competition have on the increase in male intrasexual competition, with its interaction with hierarchical steepness and the degree of female dominance over males. This could be done by testing the role of sex ratio alongside other causes of mating competition such as number of fertile females and mating seasons, in relation to competition among males, hierarchical steepness and partial female dominance over males.

Data availability statement

The data and R script to replicate results of this manuscript are available at https://doi.org/10.34894/IMWDGX.

Ethics statement

This animal study was reviewed and approved by Ezemvelo KZN Wildlife, South Africa.

Author contributions

CH and TS contributed to conception and design of the study. TS wrote the first draft of the manuscript and performed statistical analyses. EW was responsible for the acquisition of data. GG supervised statistical analyses. All authors contributed to interpretation of data, manuscript revision, and read and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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Adult sex ratios and partial dominance of females over males in the rock hyrax

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Competition in group-living animals often results in a dominance hierarchy. The sex that is larger (usually the males) generally dominates the one that is smaller (the females). In certain species, however, despite being smaller, the females dominate several males. Female dominance over males may here arise from the self-reinforcing effects of winning and losing fights, the so-called winner-loser effect, as demonstrated in the model DomWorld. In the model, females may become dominant over more males when the percentage of males in the group is higher due to the higher intensity of aggression of males than females combined with the higher frequency of male–male fights. This association between female dominance and the percentage of adult males in the group has been confirmed in several primate species. Since in the model DomWorld this association requires few assumptions, it should be tested beyond primates. In the present study, we investigated it in the group-living rock hyrax (*Procavia capensis*), because it fulfilled most requirements. We used data on adults from six groups, collected over 20 years in natural colonies in Israel. We confirmed that body weight and intensity of aggression was greater in males than females. Three measurements indicated that females dominated *ca.* 70% of the males. Unexpectedly, only in the data where groups comprised several males, female dominance over males was shown to increase with male percentage, but not when including (the many) years in which groups comprised a single male. We attribute this non significance to the limited male–male interactions. One of the requirements of DomWorld is that individuals live in permanent groups, but in rock hyrax there were also bachelor males, that were not permanently associated with a group. Thus, we expected and confirmed that there was no association between the percentage of males and female dominance over males when including them. In conclusion, our results support the hypothesis that the winner-loser effect contributes to the dominance of females over males, and the association between the percentage of males in a group and female dominance over males requires an extra criterion: that most groups contain multiple males.

KEYWORDS

female dominance, *Procavia capensis*, self-organisation, sex ratio, intersexual dominance, winner-loser effect, computational model

Introduction

Competitive interactions among individuals in a group often result in a dominance hierarchy (Drews, 1993). When the hierarchy is steep, meaning that differences in rank among individuals are large, the society is despotic. Here, the dominant individuals have more access to resources than the subordinates. In an egalitarian society, in contrast, individuals are similar in rank and have comparable access to resources (Vehrencamp, 1983). Higher rank has been linked to individual attributes, such as larger body size (Beacham, 1988). However, females sometimes dominate several males despite the smaller body size of females, such as in macaques (*Macaca* spp.; Hemelrijk et al., 2008), vervet monkeys (*Chlorocebus pygerythrus*; Hemelrijk et al., 2020a,b), and capuchin monkeys (*Sapajus libidinosus; S. nigritus,* and *S. xanthosternos*; Izar et al., 2021). Causes of dominance rank are, thus, more complex and do not depend merely on body size. For instance, dominance rank may depend on other processes such as coalitional support (Vullioud et al., 2019), or the self-reinforcing effect of winning and losing competitive interactions (Franz et al., 2015), the so-called "winner-loser effect," which is prevalent in the animal kingdom (Hsu et al., 2006). The winner-loser effect causes winners to be more likely to win subsequent fights and losers to be more likely to lose them. In the present paper we examine how the winner-loser effect influences dominance between sexes.

The consequences of these self-reinforcing effects regarding both dominance style and intersexual dominance have been demonstrated in the computational model DomWorld (Hemelrijk, 1999). In this model, individuals aggregate and may attack when they are near others. They are more likely to attack when their own dominance value (representing their fighting capacity) is relatively high compared to that of their opponent. After a fight is decided, the dominance value of the winner increases, enhancing the likelihood that in the next fight it will win again and that of the victim decreases, making it more likely that the loser will be beaten in the next fight. The model demonstrates that a dominance hierarchy will develop even if all individuals start with the same initial dominance value (Hogeweg, 1988; Hemelrijk, 1999).

Regarding dominance style, the model demonstrates that when aggression is fierce (such as biting) the hierarchy becomes steeper, resembling that of a despotic society. This arises because fierce aggression has greater impact than mild aggression (such as staring or threatening) on the subsequent winning tendency of the opponents. When aggression is mild, the impact of conflicts is small and the hierarchy differentiates little, resembling that of an egalitarian society (Vehrencamp, 1983; Hemelrijk, 1999).

Regarding intersexual dominance, the model DomWorld demonstrates that even though the fighting capacity of females is initially lower than that of males (reflecting the females' smaller body size and lower intensity of aggression), some females may still become dominant over some males (Hemelrijk et al., 2003). This occurs, however, only when aggression intensity is high, because the hierarchy differentiates strongly due to the high impact of fights and this causes overlap between the dominance of males and females. If aggression intensity is weak, fight outcomes have little impact on the hierarchy and the initially more powerful males remain dominant over all the females. Thus, DomWorld demonstrates that female dominance is stronger in species with more intense aggression. This has been confirmed in macaques (Hemelrijk et al., 2008). The model also reveals that female dominance over males increases with the percentage of males in the group (Hemelrijk et al., 2008). This we refer to as the self-organisation hypothesis. It is explained by a higher percentage of males resulting in a relatively higher percentage of male–male fights. Through the higher intensity of aggression by males than females, this higher percentage of male–male fights leads to stronger female dominance over males because more males are defeated and sink to a lower rank than some females. This association between the percentage of males and female dominance in the group has been confirmed in empirical studies of macaques (Hemelrijk et al., 2008), vervet monkeys (Hemelrijk et al., 2020b), and capuchin monkeys (Izar et al., 2021).

The assumptions in DomWorld underlying the self-organisation hypothesis, namely the association between female dominance and percentage of males, are that: (1) individuals live permanently in a group; (2) the agonistic interactions result in the winner-loser effect; (3) the initially greater fighting capacity of males than females (e.g., in real animals body weight of males is greater than that of females); (4) the intensity of aggression is high; (5) and higher in males than females; and (6) the range of adult sex ratios across groups is sufficiently large.

Although these assumptions are expected to be met in many group-living species, this association has not been tested to date beyond primates. Therefore, in the present study we investigate natural groups of rock hyrax (*Procavia capensis*) in Ein Gedi, Israel. The rock hyrax fulfils many of the requirements of the DomWorld model: individuals live in permanent groups with both sexes, aggression is sometimes intense, males are slightly larger than females on average (Koren, 2006), and these groups show a large range of sex ratios. Although the winner-loser effect has not been studied in this species, it has been shown in all taxa where it has been tested, namely, insects, crustacean, amphibia, reptilia, fish, birds and mammals, including humans (Hsu et al., 2006). Besides, in the present study, we confirmed that the body size and intensity of aggression in males of rock hyrax is greater than in females. We quantified female dominance over males and studied whether with a greater percentage of males in the group there was an increase in the dominance of females over males and the percentage of male–male fights of all fights of males with adults. As an alternative, we also investigated whether the dominance of females over males was greater when the percentage of young males or "late dispersers" in the group was higher, because these are males over which females could dominate easily.

The groups of rock hyrax comprise not only resident males (that reside in a group for a few years), but also so-called "bachelor" males. Bachelor males often reside alone, occasionally in all-male groups and sometimes interact with groups, but are not permanently associated with a specific group (Koren, 2000).

Herewith, bachelor males do not fulfil the requirement from DomWorld of permanent group living (requirement 1). Thus, we expected no association between the percentage of males and female dominance over males when including bachelor males.

Materials and methods

Study animals, field procedures and behavioural observations at the Ein Gedi Nature Reserve in Israel

The rock hyrax belongs to the order hyracoidea (Afrotheria; Murata et al., 2003; Springer et al., 1997). This species is widely distributed across Africa and the Middle East, where it inhabits mostly rocky areas. Males and females reach sexual maturity at the age of 17 to 24 months (Hoeck et al., 1982) and can live up to 12 years (Mendelssohn, 1965; Glover and Sale, 1968). Most adolescent males disperse upon reaching sexual maturity (Hoeck et al., 1982), with those males that remain in their natal group past sexual maturity being referred to as "late-dispersers" (Koren, 2006). When the males disperse, they either join a new group as residents or remain on the periphery of groups as "bachelors," mostly sleeping alone or on rare occasions in all-male bachelor groups (Koren, 2000). Resident males reside in a group of females for an average of 3 years (maximum 5) before leaving the group and being replaced by another male. In both sexes aggressive behaviour is sometimes intense, such as biting, fighting and chasing, even killing has been observed (Supplementary Table S1). Both males and females have long incisors (i.e., tusks), that can inflict fatal wounds (LK pers. observation). Rock hyraxes breed seasonally (Mendelssohn, 1965; Millar, 1971; Frey and Miller, 1972; Neaves, 1973), with synchronised parturition (Mendelssohn, 1965; Sale, 1965). Although resident males guard their mates and bachelor males also sire offspring (Bar Ziv et al., 2016).

Rock hyraxes were studied at the Ein Gedi Nature Reserve, (31°28′N, 35°24′E), near the Dead Sea (Supplementary Figure S1A; Supplementary material). The reserve comprises two deep gorges, David and Arugot. Field seasons lasted for 5–6 months each year, from March to September. Data were collected yearly between 2000 and 2019 on 1,213 days on about 4 h a day. Data from 2006 and 2019 are missing due to insufficient observations. The total population size was between 500 and 1,000 individuals (Barocas et al., 2011). Six groups were studied (7 groups when including bachelors, Table 1; Supplementary Table S3; Supplementary Figure S1B). Since we studied each group over several years, we refer to these data-points as group-years. Data were collected using binoculars, a telescope, and paper and pencil (Supplementary Table S2). All individuals were recognisable by marking them with a subcutaneous tag, earrings, and a collar (weighing 5 g). To mark the individuals (including females, resident males and bachelor males) they were caught yearly using live box traps and anaesthetized with ketamine hydrochloride. Following the protocols established by Koren et al. (2006, 2009), groups were observed mostly in the morning, from first light to noon; and, after a period of when hyrax were resting because of the heat, they were observed for ~2 h in the later afternoon until dusk. Observers sat at fixed points and scanned the area for rock hyrax. Once a group was detected, it was followed until it retreated underground because of high temperatures. Observation time was distributed approximately equally over all groups.

We sampled agonistic interactions by all occurrences, because the activity level was low and the group sizes were small, and we continuously could see all individuals of a group. We recorded the behaviour of resident and bachelor males at a similar frequency.

We defined individuals to be adult when they were older than 2 years and focused on their interactions within the same group. Because we recorded behaviours with several observers, at the beginning of each season we practised observing the same interactions to train all people to note behaviour in the same way. For all agonistic interactions we recorded the initiator of the interaction (namely the one that approached the other), the receiver, the outcome of the fight (the loser being the one who retreated or fled and the other one being the winner) and the agonistic behaviour of both opponents. An interaction ends with one individual walking away or running away. Agonistic acts involved elements of the ethogram, namely attack, fight, chase, flee, displace, retreat, threat, bite and kill (see Supplementary Table S1). Agonistic interactions were subdivided into fierce and mild, with attacking, chasing, biting, fighting, and killing being counted as fierce and threatening, and displacing as mild. If several agonistic elements were observed in an interaction, we categorised the interaction by the element of the highest intensity. The order of the elements, from lowest to highest intensity was: displace, threat, attack, chase, bite, fight, and kill. When comparing the intensity of aggression between the sexes we used the proportion of fights per individual that were of high intensity of all fights that an individual initiated.

Rank order and female dominance over males

We determined the rank order in the dominance hierarchy of adults of both sexes in each group in each year we studied it (group-year), using the Average Dominance Index, ADI, namely the average percentage of conflicts with which each adult was victorious over all its adult opponents (Hemelrijk et al., 2005). It is similar to David's Score (Gammell et al., 2003), but has a better treatment of missing values as is shown in studies of hierarchical steepness (Saccà et al., 2022) and its computation is simpler and easier to interpret. The degree of dominance of females over males was measured using the Female Dominance Index, FDI, which gives the percentage of males that rank below females on average (Hemelrijk et al., 2008, 2020a). As a robustness measure of the Female Dominance Index, FDI, we calculated two additional measures of female dominance over males: (a) the average percentage per group-year that each female wins fights from each

of her male opponents; and (b) the percentage of intersexual dyads (with interactions) in which females won more than half of their fights.

Statistical analysis

To derive a dominance hierarchy, we considered interactions within groups among adult individuals (older than 2 years) that were resident in a group, ignoring bachelor males because they are not integrated in the group. Note that we have only included groups if they contained both sexes, and if at least three individuals were involved in at least one competitive interaction with an opponent.

Data were tested for normality by conducting Shapiro–Wilk tests and examining qq-plots. Where data were normally distributed, parametric tests were used. Otherwise non-parametric tests were used. Data analysis were done in R version 4.1.2 (R Core Team, 2021) and we used packages glmmTMB (Brooks et al., 2017) to conduct GLMMs and LMMs and tested their goodness-of-fit by comparing residuals with simulated residuals using the package DHARMa (Hartig, 2019). Likelihood ratio tests were performed, comparing full models to null models (containing only the intercept and random effects; package lmtest Zeileis and Hothorn, 2002).

We tested the difference in weight and intensity of aggression between females and males using linear mixed models, with ID as a random effect. The relationship between the percentage of males, the Female Dominance Index and percentage of male–male fights (number of fights initiated by males against other males divided by the total number of fights initiated by males towards either male or female adults) were tested using a GLMM with a beta-binomial family to account for possible over-dispersion and with group as a random effect. We investigated whether the presence of late-dispersers in group-years influenced our results by testing in group-years with multiple males, whether the percentage of late-dispersing males in the group was associated with the degree of female dominance (FDI) or the percentage of males. We did this by performing a binomial GLMM with group as a random effect. For this model we included an observation level random effect (OLRE) to reduce over-dispersion (Harrison, 2015). For all linear or general models, we report the estimate and standard error. For significance, we report the likelihood ratio test between the full and null models.

Results

Resident group members

Partial dominance of females over males became clear in several ways. The position of females in the dominance hierarchy among adults (Figure 1), reveals that in 18 of the 27 group-years one or more females had occupied the alpha position exclusively; in 7 cases females shared the alpha position with one or more males; and only in a single case did a male hold the alpha position alone. On average, females dominated 69% of the resident males (Female Dominance Index; Tables 1, 2), meaning that they were subordinate to only 31% of the resident males. The other two measures, based on the percentage of intersexual fights won, provided similar results: females dominated 72% and 67% of the males (Table 2). In our remaining analyses we used the Female Dominance Index, FDI, because this measure was also used in setting up the predictions of DomWorld (Hemelrijk et al., 2008) and testing them in primates (Hemelrijk et al., 2008, 2020b; Izar et al., 2021) and the FDI realistically incorporates both intra- and intersexual interactions when determining female dominance over males. The dominance hierarchy among resident group members shows numerous shared ranks (Figure 1), probably due to the low number of interactions. The frequency of agonistic interactions among adults is low as is typical of this species, per group-year it ranges from 2 interactions in small groups of 3 individuals to 28 in a group of 7 (Table 1).

The requirements of DomWorld regarding sexual dimorphism held true: namely, compared to females, resident males weighed more (average weight of males 2.76 ± 0.07 and of females 2.23 ± 0.03 kg, LMM, ID as random effect, $n_{\text{Males}} = 25$, $n_{\text{Females}} = 85$, estimate (SE) = 0.52 (0.08), $z = 6.12$, LRT: $\chi^2 = 29.91$, $p < 0.001$, Supplementary Figure S2A) and the percentage of fights of high intensity initiated by males was greater than that by females (binomial GLMM with ID as random effect $n_{\text{Males}} = 20$, $n_{\text{Females}} = 80$, estimate (SE) = 1.20 (0.46), LRT: $\chi^2 = 6.43$, $p = 0.01$, Supplementary Figure S2B).

Unexpectedly, the Female Dominance Index, FDI, did not increase significantly with the percentage of males in the group (test 1 in Table 3; Figure 2A), but the percentage of male–male fights did (test 2 in Table 3; Figure 2B). The relationship between the percentage of males in the group and the Female Dominance Index may have been nonsignificant due to the low absolute number of male–male interactions. This was a consequence of the high number of group-years (17 of the 27 group-years) comprising a single male only and the low number of group-years (10) comprising more than a single male (namely 2 or 3 males; Table 1; Figure 2B).

When limiting our analyses to group-years with multiple males, by excluding single male group-years (Figures 2C,D), the Female Dominance Index significantly increased with the percentage of males (test 3 in Table 3; Figure 2C). However, the percentage of male–male fights did not increase with the percentage of males in the group (test 4 in Table 3; Figure 2D).

Alternatively, female dominance may increase with a higher percentage of males in the group because in groups with multiple males, some could be young males that have not yet dispersed (late-dispersers) and females may be dominant over these males. We did not find evidence for this type of dominance since in group-years containing multiple males (which we will refer to as multi-male group-years), late dispersers were neither lower in rank than residents (t-test, $n_{\text{MaleResidents}} = 13$, $n_{\text{Late-disperser Males}} = 10$,

TABLE 1 Summary results of agonistic interactions among adults in rock hyrax groups in Ein Gedi, Israel.

Site	Group	Year	Number of males	Number of females	Percentage of males (%)	FDI (%)	Number of interactions	Percentage MM/MA
Arugot	Cube	2012	1	3	25	50	6	0
Arugot	Cube	2013	2	8	20	47	23	100
Arugot	Cube	2015	1	6	14	92	28	NA
Arugot	Cube	2017	1	3	25	100	8	0
Arugot	Gal	2000	2	3	40	100	7	NA
Arugot	Gal	2001	1	2	33	100	2	NA
David	Hill	2004	1	2	33	100	2	NA
David	Hill	2014	1	2	33	25	4	0
David	Hill	2015	2	6	25	58	14	0
David	Hill	2017	1	3	25	33	6	0
David	Hill	2018	3	2	60	100	8	100
David	Hill	2019	3	1	75	83	3	100
Arugot	Isiim	2000	1	7	13	71	12	0
Arugot	Isiim	2002	2	3	40	100	3	NA
Arugot	Isiim	2008	1	4	20	88	3	NA
Arugot	Isiim	2009	3	7	30	38	6	50
Arugot	Isiim	2010	1	5	17	90	4	NA
Arugot	Isiim	2017	1	3	25	67	8	0
Arugot	Isiim	2018	1	4	20	75	7	0
Arugot	Sukkot	2000	1	6	14	8	11	0
Arugot	Sukkot	2002	1	4	20	88	4	NA
Arugot	Sukkot	2003	3	6	33	69	7	0
Arugot	Sukkot	2004	2	2	50	50	2	100
Arugot	Sukkot	2009	1	6	14	75	5	NA
Arugot	Sukkot	2017	2	3	40	42	8	0
David	Window	2017	1	3	25	100	6	NA
David	Window	2018	1	3	25	17	3	0
Average			1.52	3.96	29	69	7.41	26

FDI, Female Dominance Index; Percentage MM/MA (fights among males from males with adults of either sex). NA indicates that there was no aggression initiated by a male. This table presents agonistic interactions among resident group members only, and does not include interactions with individuals from other groups or bachelor males.

$t = -0.74$, df = 18.99, $p = 0.47$) nor did the degree of female dominance over males increase with the percentage of late dispersers (binomial GLMM with group as random effect, multi-male group-years $n = 10$, estimate (SE) = 1.9 (1.46), LRT: $\chi^2 = 1.62$, $p = 0.20$).

Including interactions with bachelor males

Because bachelor males did not live permanently in groups (requirement 1 of DomWorld) but interacted now and then with a few groups (Supplementary Figure S3), we did not expect a significant correlation between the Female Dominance Index and proportion of males when including bachelor males.

We confirm that when adding the interactions with bachelor males, the correlation between the Female Dominance Index and proportion of males was not significant (test 5 in Table 3; Figure 3A), also not when only group-years with several males were used (40 group-years, test 7 in Table 3; Figure 3C); nor was the percentage of males related to the percentage of male–male fights (test 6, 8 in Table 3; Figures 3B, 3D).

Note that including interactions with bachelor males reduced the degree to which females were dominant over males in all three measurements (Table 2; Supplementary Table S3).

Discussion

The results of the present study support the earlier findings that in the rock hyrax the females dominate most of the males (Koren, 2000; Koren et al., 2006; Koren and Geffen, 2009). Here we show that this dominance exists despite the females weighing less and displaying milder aggression than the males do. Females dominated on average 69% of the males [according to the Female Dominance Index (Hemelrijk et al., 2008, 2020b; Izar et al.,

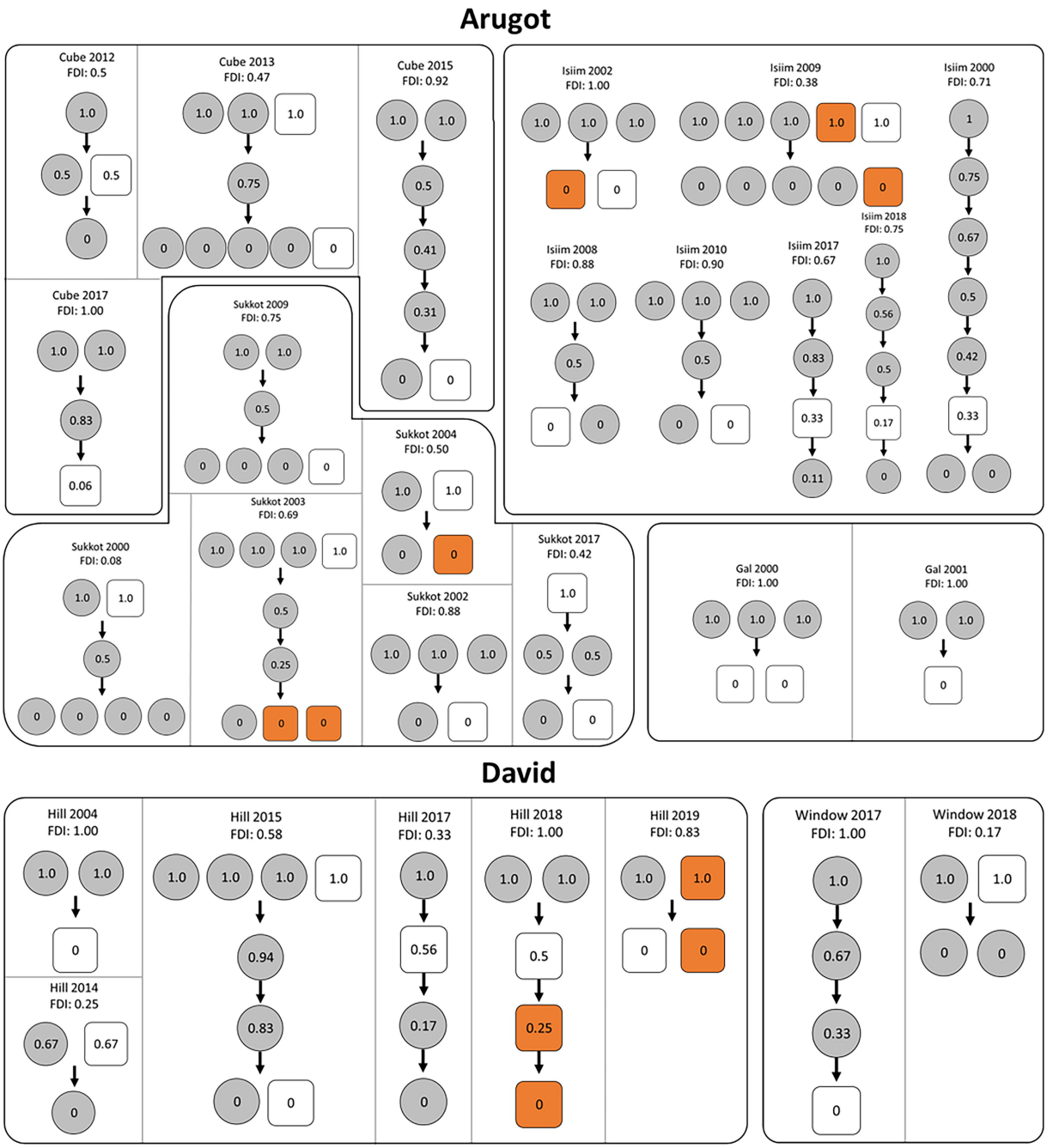

FIGURE 1
Dominance hierarchies in groups of rock hyrax among adults of both sexes per group-year at two sites, Arugot and David in Ein Gedi, Israel. Partitions indicate name of the group and year of study. FDI represents the Female Dominance Index per group-year. Circles represent females and squares represent males. The average dominance index of each individual is shown in the circles and squares. Late dispersers (males) are indicated in orange.

2021)]. This value is consistent with that of our other two measurements, which only included intersexual fights. Such consistency among different measures of female dominance over males has recently been found in a theoretical study and an empirical study on several species of primates, rock hyrax and hyenas (Seex et al., Accepted/In press; Kappeler et al., 2022, this issue). Note that despite the similar values of the different types of measurement, the Female Dominance Index is the most appropriate tool because it was used in the predictions of DomWorld and it is based on the dominance hierarchy including both sexes. Since interactions among individuals of the same sex as well as the opposite sex are likely to lead to the winner-loser

TABLE 2 Partial female dominance over males according to three different measurements for interactions between adult group members only and group members with bachelor males.

Measure of female dominance	Female Dominance Index (FDI)	Average percentage of intersexual fights won by females per male opponent	Percentage of intersexual dyads that interacted in which females won >50%
Within groups only	69%	72%	67%
Including bachelor males	57%	54%	49%

TABLE 3 Statistical results (GLMM) for the relationship between the percentage of males (predictor) and either the Female Dominance Index (FDI) or the percentage of male–male fights out of all fights involving males with other adult hyraxes of either sex (dependent variable).

	Test	*N*	Estimate (SE)	LR χ^2_1	*p*
	Residents only				
	All groups				
1	FDI ~ Percentage of males	27	2.00 (1.78)	1.33	0.25
2	% males–% MM fights	17	12.18 (5.83)	8.16	0.001
	Multi-male groups only				
3	FDI–Percentage of males	10	5.01 (2.48)	3.79	0.05
4	% males–% MM fights	8	6.59 (5.45)	2.01	0.16
	Residents and bachelors				
	All groups				
5	FDI–Percentage of males	45	−1.86 (1.30)	2.07	0.15
6	% males–% MM fights	40	3.44 (2.06)	2.93	0.09
	Multi-male groups only				
7	FDI–Percentage of males	40	−1.82 (1.409)	1.71	0.19
8	% males–% MM fights	38	2.87 (2.1)	1.93	0.16

Results are given for all group-years and for only those with multiple males. This is shown for interactions among residents within groups only, as well as for interactions between resident group members and bachelor males.

effect, both will impact each individual's ability to win in subsequent fights and therefore the position of each individual (of either sex) in the dominance hierarchy.

In the subset of group-years of rock hyrax that included multiple males, female dominance over males increased with the percentage of males in the group. In line with the self-organisation hypothesis from the DomWorld model (Hemelrijk et al., 2008), this association may arise in rock hyrax from the dynamics of the self-reinforcing effects of winning and losing fights. The self-organisation hypothesis argues that when the percentage of males in the group is higher, females become dominant over more males because of the relatively more frequent male–male fights. This is due to the higher intensity of aggression of males than females. When male–male fights are more numerous, males will be beaten by other males more often, resulting in more males dropping in rank, even below some females (Hemelrijk et al., 2020a; Izar et al., 2021). Yet, the relationship between the percentage of male–male fights and the percentage of males in groups with more than one male was not significant in rock hyrax. This lack of significance may be due to the small sample size of only eight group-years, and the number of males per group-year being small (two or three males). Note that this relationship was significant in the 17 group-years when including groups with a single male.

The relationship between the percentage of males in the group and the Female Dominance Index was significant when considering only multi-male groups. We must note, however, that multi-male groups are rare in the rock hyrax and single-male groups are the norm (Koren, 2006). Thus, in our study, the range in sex ratios among group-years was due to the large range in the number of females rather than males. Our study indicates that an additional, new, seventh requirement is necessary to establish the self-organisation hypothesis of female dominance over males (Hemelrijk et al., 2008). Not only should: (1) individuals live in permanent groups; (2) the agonistic interactions result in the winner-loser effect; (3) body size be larger in males than females; (4) the intensity of aggression be high; (5) and be higher in males than females; and (6) the range of adult sex ratios across groups be sufficiently large; but also, (7) most groups should include multiple males. This is important because the presence of more males increases the average aggression intensity and thus the hierarchical differentiation, which causes stronger overlap in dominance

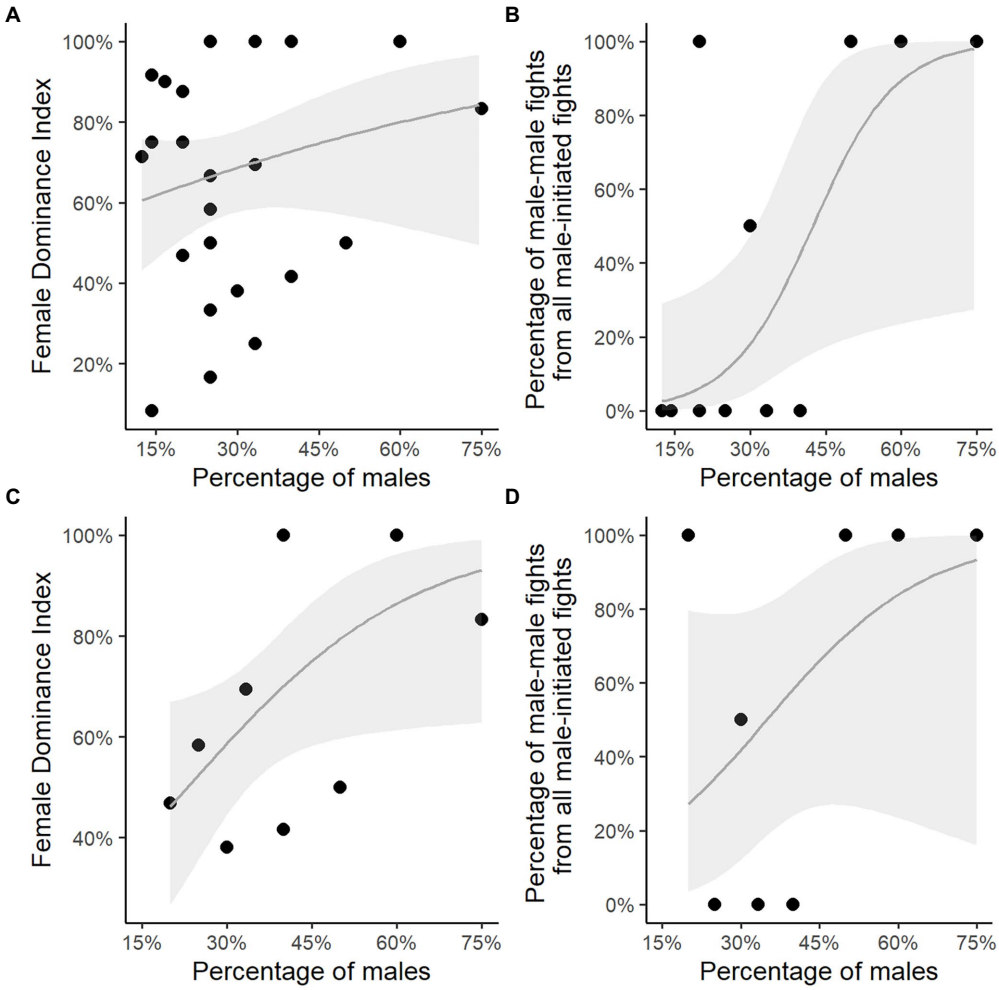

FIGURE 2
Percentage of resident males in rock hyrax groups versus the Female Dominance Index and the percentage of male–male fights. Percentage of resident males in groups with a single male or multiple males versus **(A)** the Female Dominance Index; **(B)** the percentage of male–male fights of male-all fights. Percentage of resident males in multi-male groups only versus **(C)** the Female Dominance Index; **(D)** the percentage of male–male fights of male-all fights. The grey line represents the fitted regression line, grey polygons represent the 95% confidence intervals.

between the sexes. Thus, logically, we do not expect any relation between female dominance and sex-ratio in species that live in one-male groups, such as hamadryas baboons.

Alternatively, female dominance over males may increase with a higher percentage of males due to a higher percentage of young "late-disperser" males. We rejected this alternative explanation because a higher percentage of late dispersers in group-years was not associated with stronger dominance of females over males, and late dispersers were not significantly lower in rank than resident males.

We confirmed that when we violated requirement 1 of permanent group-living, of the self-organisation hypothesis of DomWorld, by including interactions with bachelor males (that were not permanently associated with the group), the relationship between the percentage of males and female dominance was not significant (also not significant when only group-years with multiple males were considered). Thus, in general, when including individuals that do not live permanently in a group, the correlation between percentage of males and female dominance over males is less likely. Thus, this correlation is less likely when dealing with groups in societies that are very loose, such as fission fusion societies where subgroups split up and merge continuously as in chimpanzees unless subgroups are larger, such as in bonobos (Furuichi, 2009).

Whether and why bachelor males in our study of rock hyrax are more dominant over females than resident males requires further investigation. According to the self-organisation hypothesis this may be because bachelor males were less often defeated by resident males, thus their dominance relative to females depended more on their body size (which is larger than that of females) than in resident males. This issue should be further explored in future studies. The self-organisation hypothesis from DomWorld was designed to predict within-group interactions and does not

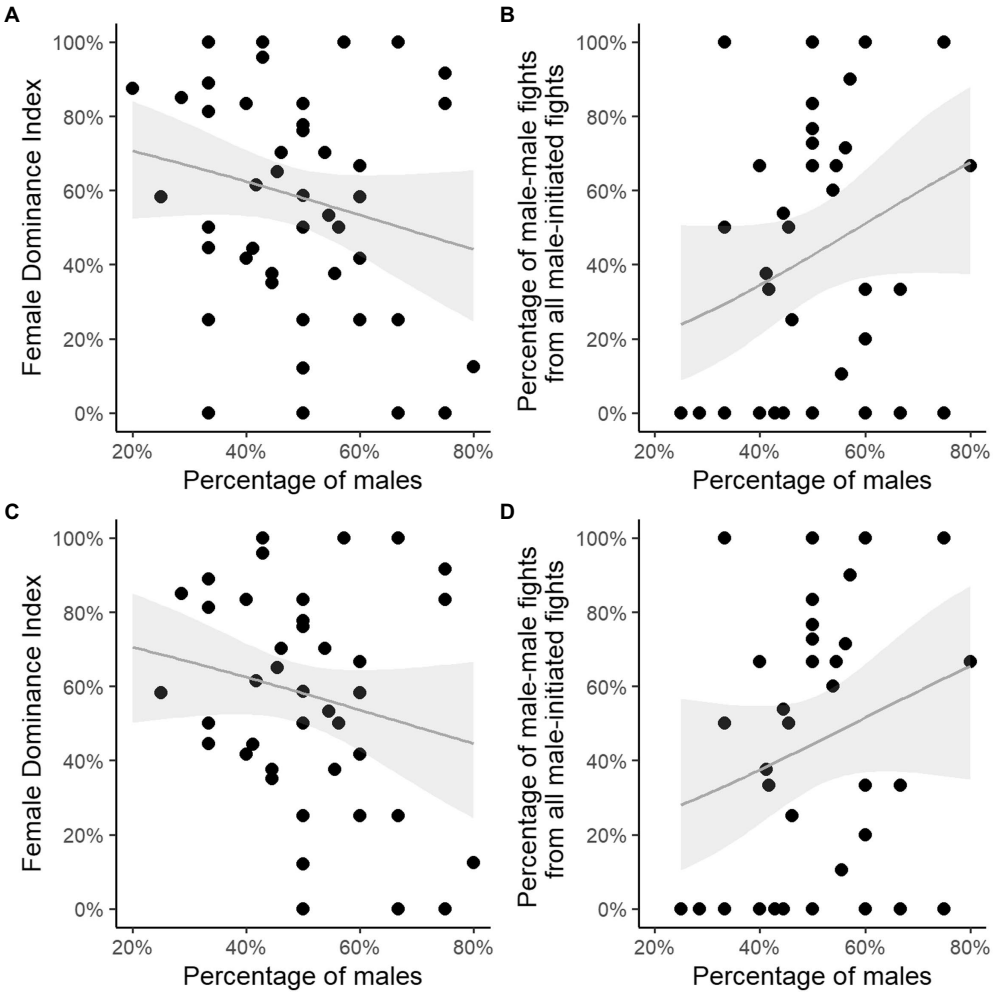

FIGURE 3
Percentage of resident plus bachelor males in groups with a single male or multiple males versus **(A)** Female Dominance Index; **(B)** percentage of male–male fights of male-all fights. Percentage of resident plus bachelor males in multi-male groups only versus **(C)** Female Dominance Index; **(D)** percentage of male–male fights of male-all fights. Grey line represents the fitted regression line, grey polygons represent the 95% confidence intervals. Note that some data-points overlap, see Table S3 for all values.

work with the inclusion of outsiders such as bachelor males. To gain more knowledge on dominance in bachelor males, detailed empirical data should be collected by focussing particularly on them. Regarding why bachelor males interact with groups, we hypothesise that they do so in particular to gain access to females. Indeed, bachelor males have been observed to copulate with females at the same rate as resident males (Bar Ziv et al., 2016).

We conclude that female dominance over males is a dynamic trait rather than a static feature (Chase, 1985; Lindquist and Chase, 2009), and may partially rely on the winner-loser effect, because it depends on the adult sex ratio in a group. We have shown that the positive relationship between the percentage of males in the group and the degree of dominance of females over males occurs in the rock hyrax and thus is not limited to primates. Because the general requirements for such a relationship, as presented in the DomWorld model, are met in many species, we expect it to be found also in other animals that are living in permanent groups.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Ethics statement

Our study was conducted under annual permits from the Israeli Nature and Parks Authority (NPA) for capturing, handling, and tagging the hyraxes at the Ein Gedi Nature Reserve (2002/14674, 2003/14674, 2004/17687, 2007/27210, 2008/31138,

2009/32871, 2010/37520, 2011/38061, 2012/38400, 2013/38803, 2017/41507, 2018/41880). All procedures performed in this study involving animals were in accordance with the ethical standards of the NPA and the state of Israel.

Author contributions

The scientific conceptualization came from CH and LK. Data were collected and provided by LK, AI, and EG. Data analyses were done by MP and LS. Figures were created by LS. The writing was done by CH with help of LS, LK, AI, and EG. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.1004919/full#supplementary-material

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Variation in Female Leverage: The Influence of Kinship and Market Effects on the Extent of Female Power Over Males in Verreaux's Sifaka

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Female mammals employ reproductive strategies (e.g., internal gestation) that result in power asymmetries specific to intersexual dyads. Because the number of eggs available for fertilization at any given time for most mammals is quite limited, having a fertilizable egg is potentially an important source of economic power for females. Control over mating opportunities is a source of intersexual leverage for female Verreaux's sifaka (*Propithecus verreauxi*). We examined economic factors thought to influence the value of mating opportunities, and, thus, the extent of female leverage: kinship and market effects. Using a longitudinal dataset of agonistic interactions collected during focal animal sampling of all adult individuals in 10 social groups from 2008 to 2019, we tested the effects of relatedness, female parity, reproductive season, and adult sex ratio (population and group) on (1) the direction of submissive signaling and (2) which sex won a contested resource. While 96% of the acts of submission were directed from males toward females, females only won a third of their conflicts with males. Thus, our study has implications for evolutionary explanations of female-biased power. If female power evolved due to their greater need for food and other resources, then intersexual conflicts would be expected to result in males more consistently relinquishing control of resources. As expected, males were more likely to chatter submissively toward successful mothers, during the mating season, and when the sex ratio was male-biased. Although females generally had less power to win a conflict when their fertilizable egg was less valuable (when they were nulliparous or unsuccessful mothers or when interacting with male kin) and with an increasing female-bias in the sex ratio, this ability to win additionally was influenced by which sex initiated the conflict. Our study demonstrates that female leverage can be influenced by the supply and demand for mating opportunities, but evoking submission does not translate into winning a resource. Indeed, intersexual power is dynamic, contextual, and dependent on the individuals in the dyad.

Keywords: female dominance, intersexual relationships, subordination, primate, lemur

INTRODUCTION

In some animal societies, females are more powerful than males. This phenomenon is often called "female dominance," but both theoretical (Hand, 1986; Smuts, 1987; Lewis, 2002, 2018, 2020) and empirical (Lewis, 2004; Surbeck and Hohmann, 2013; Young et al., 2017; Voyt et al., 2019) work suggests that female power over males can also be leverage, i.e., where female power over males arises from an asymmetry in intrinsic economic resources rather than an asymmetry in fighting abilities (Hand, 1986; Lewis, 2002, 2018, 2020). For example, the reproductive cycles, internal gestation, and lactation of female mammals can result in operational sex ratios that are highly male skewed (Emlen and Oring, 1977), i.e., where the number of sexually active males in a population greatly exceeds the number of sexually available females. Under this situation, having a fertilizable egg can be an important source of economic power (i.e., leverage) for females (Noë et al., 1991; Lewis, 2002, 2004, 2018, 2020). Indeed, fertilization potential (a source of leverage) predicts intersexual status in sifaka, but sexual size dimorphism within a dyad (a source of dominance) does not (Voyt et al., 2019). Similarly, mating opportunities are a source of female leverage in bonobos that results in reduced intersexual aggression by males (Surbeck and Hohmann, 2013). Thus, species exhibiting a female-biased power structure can exhibit female dominance, such as in spotted hyenas where intersexual power is determined by the combined fighting abilities of coalitions (Vullioud et al., 2019), female leverage, such as in bonobos and sifaka, or a combination of both types of female power. In fact, these and other species likely exhibit multiple types of power simultaneously.

Empirical research on leverage suggests that it may be central to understanding female-biased power in these societies, especially if the extent of female economic power varies with the value of the commodity being offered (Noë and Hammerstein, 1994, 1995; Lewis, 2002). For example, bonobo males do not exhibit aggression toward females when mating has a high probability of resulting in a conception (Surbeck and Hohmann, 2013), suggesting that the value of a female as a mating partner is discounted at other times. Consistent with the hypothesis that the value of a female's fertilizable egg varies with her experience and success at mothering, male sifaka are more submissive toward successful mothers than nulliparous females or parous females who have not yet successfully reared an infant, indicating that successful mothers have more leverage than other females in their relationships with males (Voyt et al., 2019). In other words, intersexual power can be highly dynamic, contextual, and dependent on the individuals in the dyad (Lewis, 2002).

Hypotheses for the evolution of female-biased power in animal societies often focus on the importance of females winning resources (e.g., Jolly, 1984; Young et al., 1990; Wright, 1999). A winner is the "contestant that expressed consummatory behavior according to its initial goal" (Drews, 1993, 285). Despite this emphasis on resources, "winning" is often assessed by whether a male is submissive toward females (Pereira et al., 1990; Pochron et al., 2003; Bolt, 2013; Hohenbrink et al., 2016; Voyt et al., 2019), with the assumption that the ability to evoke submission and the ability to command priority of access to resources are equivalent. However, eliciting a submissive signal and usurping resources are different scopes of power (*sensu* Lewis, 2002: the outcomes that can be achieved due to the power asymmetry in the dyadic relationship). Additionally, winning a particular contest may be determined by either a power asymmetry (difference in fighting ability or difference in inalienable resources) or an asymmetry in motivational state independent of the power relationship (Schjelderup-Ebbe, 1922; Lewis, 2002, 2022; Allen et al., 2016). Some authors do consider motivation along with dominance and leverage to explain power (e.g., Surbeck and Hohmann, 2013; Vermande and Sterck, 2020), however, we consider motivation to be an orthogonal axis relevant to explaining the outcome of particular *interactions* but not a source of power in a *relationship* (Lewis, 2002, 2022). While the term "motivation" can be used to describe how an individual might be driven to seek resources due to evolutionary strategies (Surbeck and Hohmann, 2013), we limit our use of the term "motivation" to refer to ephemeral physiological states such as hunger, thirst, or exhaustion (see also Allen et al., 2016). Hypotheses about the evolution of female-biased power endeavor to explain the pattern of asymmetries in intersexual relationships (*sensu* Hinde, 1976) rather than the outcomes of any single conflict.

The aim of this study was to test the hypothesis that female leverage in intersexual dyads varies with the value of mating opportunities in Verreaux's sifaka using novel factors that investigate different levels of commodity value. First, female leverage over males may vary with kinship. The value of a mating opportunity with close kin is expected to be lower than the value of an opportunity with an unrelated individual because inbreeding can increase the chance of offspring being homozygous for deleterious alleles (Charlesworth and Charlesworth, 1999). Indeed, animals often have strategies to avoid mating with close kin (Pusey and Wolf, 1996). If intersexual power is based primarily on female control over mating opportunities (i.e., access to her fertilizable egg), then females are expected to have more power over unrelated males than male kin. Nevertheless, inbred offspring can potentially contribute to fitness and can even be preferred due to the inclusive fitness benefits (Kokko and Ots, 2006; Puurtinen, 2011). Hence mating with close kin may still occur (Szulkin et al., 2013). Consequently, control over mating opportunities may be a source of female leverage in dyads with male kin, albeit to a lesser extent than with unrelated males. In other words, females may only have leverage over some males and not others because females may be low-value mates for a subset of the male population.

Second, the proportion of females in a population may influence the extent of female leverage (Lewis, 2004; Norscia et al., 2009; Noë, 2017) because the supply and demand of estrous females can potentially affect the value of mating opportunities (Noë et al., 1991). Female power increases as the proportion of males in the group increases in simulated and wild monkey studies (Hemelrijk et al., 2008; Izar et al., 2021). If female power is based on control over mating opportunities, then females are expected to have greater power when fewer other fertilizable females and more reproductively available males are present in a population (Noë et al., 1991; Noë, 2017). When mammals live

in permanent social groups, their mating options also may be mostly limited to the members of their social group (Isvaran and Clutton-Brock, 2007). Thus, the ratio of fertilizable females to males within the social group (as opposed to in the population at large) may also influence female leverage in intersexual dyads.

Sifaka are folivorous lemurs (Richard, 1978; Lewis and Lawler, 2013) that live in small, cohesive social groups containing 0 to 3 adult individuals of each sex (Richard et al., 1991; Lewis and van Schaik, 2007). Sex ratios can be highly variable between groups and in the same group across time (Richard et al., 1991; Lewis and van Schaik, 2007; Leimberger and Lewis, 2017). While both sexes can disperse, dispersal is male-biased (Richard et al., 1993; Leimberger and Lewis, 2017). Sifaka societies are characterized by a female-biased power structure (*sensu* Lewis, 2018), often referred to as "female dominance" (Richard, 1987; Brockman, 1994, 1999). Their highly seasonal reproduction and short estrus duration (0.5–96 h/year: Brockman, 1999), combined with little to no sexual size dimorphism (Lewis and Kappeler, 2005), leads to females having leverage over males (Lewis, 2004, 2020; Voyt et al., 2019). Sifaka chatter vocalizations can be an immediate signal of submission in response to aggression or a spontaneous signal about the general power status in the relationship (Lewis, 2019), depending on whether it is provoked (Flack and de Waal, 2007). Interestingly, male sifaka frequently chatter without provocation to other males but chatter submissively to females often after receiving aggression (Lewis, 2019). Moreover, female sifaka are less likely to usurp a male's resources if he chatters without provocation (Lewis, 2019). The combination of dynamic grouping patterns and power relationships in Verreaux's sifaka provide an opportunity to study how the scope (i.e., the outcomes that can be evoked) of female power (*sensu* Lewis, 2002, 2020, 2022) fluctuates with the value of their fertilizable eggs and the concomitant leverage that extends.

Using more than a decade of longitudinal behavioral, demographic, and genetic data collected for Verreaux's sifaka living in multiple social groups in the Kirindy Mitea National Park of western Madagascar, we tested the hypotheses that kinship and female scarcity influence the extent of female leverage over males. The natural variation within and across social groups in our longitudinal dataset facilitates an examination of the relational aspect of power and how it varies across dyads. We examined dyadic social interactions involving male-female dyads and predicted that (1) males are less likely to be submissive to female kin than to other females and that (2) males are more likely to win conflicts with female kin than other females because mating opportunities with related females should be less valuable. We further predicted that males are more likely to be submissive and less likely to win conflicts with females when (3) population and (4) group adult sex ratios are male-biased because the supply of mating opportunities is lower when fewer reproductively mature females are available. Similar to previous studies (Voyt et al., 2019), we further predicted that (5) males submit most to parous females who have successfully reared an offspring and that (6) males win less when interacting with successful mothers than with nulliparous or unsuccessful parous females. Finally, because the value of a mating opportunity might be discounted when a female is unlikely to be in estrus, we also predicted that (7) males are less likely to be submissive and (8) more likely to win encounters outside of the mating season than during the mating season.

MATERIALS AND METHODS

Study Population

We studied Verreaux's sifaka at the Ankoatsifaka Research Station (20°47'17"S, 44°10'0"E) in the dry, deciduous forest of Kirindy Mitea National Park in western Madagascar. This highly seasonal forest experiences substantial variation in rainfall across years (range: 374–1,577 mm), but averages 850 mm annually, mostly in January and February (Lewis and Axel, 2019). A grid system of trails every 25 m is maintained within the 1-km^2 study area to facilitate observations. Because the forest is not very tall (emergent trees are 8–18 m tall: Lewis and Bannar-Martin, 2012) and sifaka spend a substantial portion of their time in the understory or canopy, detailed social interactions can be observed easily.

All residents in multiple social groups within the study area and some individuals residing in neighboring groups were identifiable with unique nylon collars and tags or radio collars (Rasambainarivo et al., 2014) and/or using natural markings. Ages either were known based on when an individual was born into a group or estimated using dental development and wear, body size, and nipple shape (for females) assessed during annual captures (Rasambainarivo et al., 2014). We studied intersexual social interactions involving all adult ($\geq$5 years) and subadult (3 and 4 years) individuals for which we had kinship data and that resided in 10 different social groups (Groups I-VI, XI-XII, Bella, Albert). Verreaux's sifaka groups can be impermanent, and focal groups were observed an average of 6.2 years (SD = 4.9) across the 12-year study period. We tested our predictions using two age groupings, one that included only adults (N = 46 individuals) and one that included both adults and subadults (aged $\geq$ 3 years, N = 22 additional individuals). We did this because sifaka are reported to sometimes be sexually active as subadults and because the age of adulthood is inconsistely applied across studies in Verreaux's sifaka (Lewis, 2008). For simplicity, we only present analysis of "adults" in the main manuscript and include our analysis of "adults + subadults" (individuals ages $\geq$ 3 years) in the **Supplementary File**.

Data Collection

Behavioral Data

We collected all occurrences of intragroup agonistic intersexual interactions during 1-h focal animal sampling sessions (Altmann, 1974) of all adult and subadult sifaka, for a total of approximately 14,000 h of observation from 2008 through 2019. Insufficient behavioral and demographic data were available for 2009–2010 because Cyclone Fanele interrupted data collection and thus were excluded from our analysis. The identity of the initiator and of the receiver was recorded for each interaction, and all behaviors occurring during the interaction were recorded as occurring either in isolation or as part of a sequence. Agonistic behaviors were defined according to the Brockman (1994) ethogram with

the following additions: "food rob +" (X tries to take the food away from Y and is successful), "food rob –" (X tries to take the food away from Y and is unsuccessful), and "snap at" (X bites in the direction of Y but does not make contact). In addition, "proximity" (a concept implicit to the definition of certain behaviors) was defined as occurring when individuals were within 1 m of each other (Lewis, 2019).

For all agonistic encounters, we scored an individual as "winning" a conflict if the other individual in the dyad moved at least 1 m away from the "winner" within 10 s of the agonistic interaction. Note that we did not limit our analysis of "winning" to the feeding context because sifaka compete for other resources in addition to food (e.g., water, space, sun, shade, grooming partners, and huddling partners). Moreover, our definition of a "win" included a broader set a behaviors than merely "supplant" [X moves toward Y, Y immediately changes location (within 5 s), X occupies the location previously held by Y: cf. Brockman, 1994)]. If neither individual withdrew after the agonistic interaction, neither individual was considered the winner and the outcome was scored as "neutral." The one exception to this rule was for the "food rob" behaviors because "food rob +" is defined as an initiator successfully gaining control of the food resource, while "food rob –" necessarily means that the initiator was not successful. Therefore, the identity of the sifaka that had control of the food resource at the end of the "food rob" behavior was scored as the winner.

Sifaka often exhibit multiple aggressive and/or submissive behaviors within an agonistic interaction. We thus used the following rules for scoring an interaction as "win" vs. "neutral" when multiple behaviors occurred in a sequence. If a social interaction began with an approach, the 10 s rule started with the time of the first non-approach agonistic behavior. If an individual used multiple types of aggressive behaviors essentially simultaneously (e.g., lunge and cuff), then we only scored the first aggressive act. However, if an individual used repeated, successive acts of aggression toward another individual (e.g., three cuffs within 10 s) and the receiver chattered submissively immediately after each individual aggressive act (e.g., cuff then chatter response, cuff then chatter response, and cuff then chatter response), we scored each aggressive act independently, with the assumption that the additional acts of aggression were needed because the first aggressive act was not successful. When animals repeatedly made a submissive chatter vocalization spontaneously (i.e., without receiving aggression within 10 s beforehand), we scored the agonistic events as independent when there was at least 5 s between the end of the first chatter and the beginning of the second chatter. To address the issue that these repeated aggressive or submissive acts are not entirely independent of one another, we assigned a corresponding proximity "bout identity" to each agonistic act and then used bout ID as a random factor in our statistical models. A proximity bout was defined as a period of time in which the members of a dyad were continuously within 1 m of each other within a given 1-h focal sample, and all behaviors occurring during this period were assigned with the same bout ID. Finally, for each agonistic interaction, we also scored the identity of the initiator of the interaction. Note that by definition, the winner of an interaction was always scored as the initiator for supplants.

Demographic Data

We conducted monthly censuses of the population in the Ankoatsifaka grid system of trails (Leimberger and Lewis, 2017; Lewis et al., 2020). In addition to locating all groups with radio collars and recording the identity of each individual present in the group, we located unmarked groups and solitary individuals by walking the trail system. While sifaka live in cohesive groups, they sometimes visit other groups, and males occasionally roam independently during the mating season (Richard et al., 1993; Brockman, 1999; Leimberger and Lewis, 2017). On the rare occasions when a known individual was not observed on the day of the census, we nonetheless retroactively added them to the census data for that month if the individual was observed during behavioral data collection within 7 days of the census.

Analyses

Predictors

We examined several key factors that we predicted might influence female intersexual leverage based on control of mating opportunities: relatedness between members of the dyad, female parity status, reproductive season, and the population and social group sex ratios. We considered dyads as "related" if the two individuals involved were either parent and offspring, full-siblings, or half-siblings and "unrelated" otherwise. We used multilocus microsatellite marker genotypes derived from either fecal or tissue DNA for 56 of the 68 individuals (aged $\geq$ 3 years) included in this study to conduct genetic assessment of parentage and relatedness between dyads. Details of the procedures used for genotyping and for evaluating parentage and estimated relatedness are discussed in Abondano (2014) and Perofsky et al. (2021). Briefly, we used DNA extracted from either fecal samples or tissue biopsies collected during captures to genotype all individuals at a set of 14 loci known to be variable in other populations of wild sifaka (Lawler et al., 2001; Rakotoarisoa et al., 2006). The average allelic diversity across loci was 10.2 $\pm$ 3.1 SD, and the average H_e across loci was 0.79 $\pm$ 0.06. We used the software Cervus (Marshall et al., 1998; Kalinowski et al., 2007) to conduct likelihood-based maternity and paternity analyses for all younger individuals, using all adult males and females sampled in the population as candidate sires and dams, respectively. For these analyses, we assumed a genotyping error rate of 1% and assumed that we had sampled 90 and 75% of candidate dams and sires, respectively. The average proportion of loci typed in our dataset was >99%. For the panel of loci, the combined PI and PI_{sib} values were 6.3×10^{-11} and 8.4×10^{-7}, respectively, indicating a very low probability that any two individuals or two full siblings could be expected to share the same multilocus genotype by chance. Based on the distribution of likelihood scores across candidate parents, the estimated confidence in all of our assignments of maternity and paternity was $\geq$95%.

We also used the software Kingroup2 (Konovalov et al., 2004) to evaluate whether, given their particular genotypes and allele frequencies in the population at each locus, the individuals comprising each dyad were more likely to be "related" or

"unrelated" using likelihood ratio tests (see Perofsky et al., 2021 for further details). Briefly, this involved generating distributions of pairwise relatedness estimates for simulated dyads of three different levels of close kinship (parent and offspring, full-siblings, or half-siblings) and for simulated unrelated pairs and then examining the relative likelihood that a given dyad is drawn from one of the close kinship categories relative to the unrelated category. We scored a pair as "related" if the magnitude of the likelihood ratio for one or more of the close kin-unrelated comparisons was associated with a p value of <0.05 across 10,000 permutations.

For 16 individuals in this study, no fecal or tissue samples were available, thus "relatedness" between these individuals and others with whom they interacted could not be assigned. After excluding these individuals, our final sample included behavioral and relatedness data for 38 adults (and 18 additional subadults; see **Supplementary Material**). We scored three levels of female parity status, building on Voyt et al. (2019): "nulliparous" (never given birth), "parous unsuccessful" (given birth but never successfully reared an infant to age 1 year), and "parous successful" (given birth and had an infant who survived to at least 1 year). Eighteen adult females could be categorized as nulliparous because we defined adult as age 5 years. The year was divided into the mating season (January–March) and non-mating season (April–December) because the value of a potential mating opportunity might be discounted when a female is unlikely to be in estrus.

Adult sex ratio was used as an estimate of supply/demand and was defined as the proportion of adult females in the group or population (cf. Richard et al., 2002) using monthly census data. The population was defined as all individuals with the Ankoatsifaka Research Station trail system and included both marked and unmarked individuals that were solitary, roaming, and group-living. We calculated population and group adult sex ratios as the number of females divided by the total number of adults. For example, the group sex ratio was calculated as the number of adult females in a group divided by the number of total adult females and males in the group, and the population sex ratio was calculated as the number of adult females in the population divided by the total number of adults in the population. Because age class of four unmarked, transient immigrants could not be determined with certainty, we calculated group and population sex ratios with all individuals of unknown age scored as adults and, again, with these individuals scored as subadults. While we ran all statistical models with individuals of unknown age scored as adults in the sex ratio calculations and then ran the same models again with unknown individuals scored as subadults, the results were essentially the same, and thus we only present the models where these individuals were coded as adults.

Because prior work suggests that the outcome of agonistic contests may be determined, in part, by who initiates an interaction (e.g., bison: Lott, 1979; chimpanzees: Wittig and Boesch, 2003), we initially included initiator sex as an additional predictor in our models focusing on who wins contests to, in effect, control for this variation. However, we found that initiator sex interacted in complex ways with several of our predictors of interest, and, thus, we ultimately decided to address the issue of initiator sex interacting with our predictors of interest by conducting separate analyses for when females initiated conflicts and when males initiated conflicts.

Statistical Analysis

Submissive Chatters

We first examined the direction of submissive chatters in intersexual dyads to assess the effects of the above factors on the scope (i.e., consequence) of female power. We ran a set of Bayesian binomial generalized linear mixed models (GLMMs) using the *brms* package (Bürkner, 2021) for the statistical programming R version 4.1.2 (RStudio Team, 2020; R Core Team, 2020). We used the direction of submissive chatter [female chatter directed at a male (0) vs. male chatter directed at a female (1)] as the binary response variable. Relatedness, female parity status, reproductive season, and either the population (Model 1a) or group (Model 1b) sex ratio were included as fixed effects of interest, and male identity, female identity, and bout ID were included as random effects. Note that for the model examining the group sex ratio (Model 1b), we included only the dyadic interactions for which the group membership was the same for both individuals. Interactions occurring during intergroup encounters or short visits were excluded. For each model we ran four independent MCMC chains for 10,000 iterations, sampling from the posterior distribution using the No-U-Turn sampler (NUTS) after a warmup period of 50% of the run. This yielded a total of 20,000 post-warmup draws, resulting in ESSs of $>2{,}400$ for all parameters.

Wins

We next examined whether and how who wins dyadic agonistic interactions is associated with factors potentially associated with female leverage, considering datasets of incidents initiated by males and those initiated by females separately, as noted above. For each of these datasets, we ran two sets of models using different binary response variables. The first considered whether the male in the interaction won the encounter (1) vs. either the female winning or the outcome being neutral (0). However, we also wanted to address the following question: when the conflict has a clear winner, was it the male or the female? Thus, the response variable for the second set of models was whether the male (1) or the female (0) in the interaction won the encounter, excluding all interactions where the outcome was neutral. Note that this second analysis utilized a reduced dataset.

Thus, we again ran a set binomial Bayesian GLMMs for each of the two response variables (Model 2 for male win vs. female win or neutral and Model 3 for male win vs. female win) using the same datasets and model variations as described above for submissive chatters, except that female initiated and male initiated interactions were analyzed separately. Male identity, female identity, and bout ID were included as random effects in all models. Again, for each model (with two exceptions) we ran four independent MCMC chains for 10,000 iterations, sampling from the posterior distribution using the NUTS sampler after a warmup period of 50% of the iterations. This process yielded a total of 20,000 post-warmup draws, ESSs of >800 for all model parameters. For two models (6a and 6b) involving male-initiated

contests and including data from subadults (see **Supplementary Material**) we ran our MCMC chains for 20,000 iterations after we found that initial runs of 10,000 iterations yielded low ESS values. With these longer runs, the total number of post-warmup draws across chains in each of these two models was 40,000, ESSs for all parameters were >490. Finally, for male-initiated contests with a winner and involving adults only (Models 5a and 5b), we excluded relatedness as a predictor variable because there were no cases in our dataset of a male initiating a contest that he won with a close female relative.

Model Diagnostics and Interpretation

For all models, we evaluated convergence using several standard methods implemented in the R package {shinystan} (Gabry and Veen, 2022), including visual examination of MCMC trace plots, graphical posterior predictive checks, and calculation of Brooks-Gelman-Rubin convergence diagnostic ("Rhat") values (Gelman and Rubin, 1992; Brooks and Gelman, 1998), as well as checks for multicollinearity among predictors of interest using variance inflation factors. Rhat values for all parameters in all "submissive chatter" models was ≤1.004 and was ≤1.008 in all "win" models. VIF values for all variables in all models were low (between 1.0 and 1.1 for all "submissive chatter" models, between 1.0 and 1.6 for all "win" models initiated by females, and between 1.0 and 3.6 for all "win" models initiated by males).

Finally, we used an HDI + ROPE approach (Kruschke, 2015, 2018; Kruschke and Liddell, 2018) to evaluate which of our variables of interest might be considered important predictors in all of our models. This approach evaluates how much of the credible interval for the posterior distribution around each parameter estimate (operationalized as the 95% HDI interval) falls within vs. outside a "region of practical equivalence" (or ROPE). The ROPE range is defined as an area around a null parameter value of zero within which, for practical purposes, values are equivalent to that null (Kruschke, 2015, 2018; Kruschke and Liddell, 2018). We calculated % in ROPE values using the *rope()* function from the R package {bayestestR} (Makowski et al., 2019). Below, we highlight as being potentially important those predictors for which <10% of the 95% HDI posterior distribution fell within the ROPE range. We note that we are explicitly not making dichotomous decisions about whether these predictors are "significant"; rather, we call attention to those predictors for which the bulk of the posterior probability distribution for their coefficient estimate under the model falls outside the ROPE range and discuss those in relation to our motivating hypotheses.

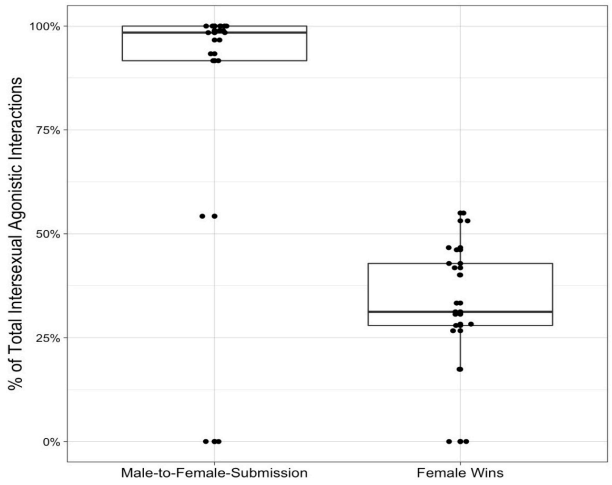

FIGURE 1 | Outcomes of agonistic interactions in intersexual Verreaux's sifaka dyads. When one individual chattered submissively, males more often chattered at females (*N* = 1,381) than females chattered at males (*N* = 56). Percent of conflicts for which females won (*N* = 639 interactions) out of the total intersexual agonistic interactions (*N* = 1,850 interactions). Lines represent medians, boxes represent 25th/75th percentiles, and whiskers represent the smallest/largest value within 1.5 times the interquartile range. Each dot represents an individual female's percentage of total submissive chatters received out of all her submissive chatter interactions, and percentage of total agonistic encounters won out of all her agonistic encounters.

RESULTS

Submissive Chatters

Out of our initial 1,931 observations of submissive chatters, we identified 1,437 instances of submissive chatters for 35 adults ($N_{females}$ = 17, N_{males} = 18) resulting in 39 dyads for which the relatedness between the initiator and the receiver could be estimated ($N_{related}$ = 2 dyads, $N_{unrelated}$ = 37). Females rarely chattered at males (only 3.9% of the total observations of chatters; **Figure 1**).

In the model including population sex ratio as a fixed effect (Model 1a), relatedness, female parity, reproductive season, and sex ratio were all potential predictors of the direction of submissive chatters (**Table 1** and **Figure 2**). The odds that a male submitted to a female were greater when the female was a close relative, when she was parous successful (as compared to nulliparous), but not when the female was parous unsuccessful. The odds that a male submitted to a female were lower outside of the mating season than during the mating season and decreased as the population sex ratio became more female-biased.

In the model including group sex ratio as a fixed effect (Model 1b), relatedness, female parity, and sex ratio were again potential predictors of the direction of submissive chatters, but reproductive season was not (**Table 1**). The odds that a male submitted to a female were greater when the female was a close relative and when the female was parous successful as compared to nulliparous females. The odds that a male submitted to a female again decreased as the group sex ratio became more female-biased (**Supplementary Table 1**).

Wins

Of the 2,530 agonistic interactions involving adults where the outcome could clearly be scored, the relatedness between the initiator and the receiver could be estimated for 35 adults ($N_{females}$ = 17, N_{males} = 18) in 1,850 of the agonistic interactions, resulting in 41 dyads ($N_{related}$ = 2 dyads, $N_{unrelated}$ = 39 dyads). Females won 34.5% of the interactions, males won 17.6%, and 47.9% of the interactions were neutral (**Figure 1**).

TABLE 1 | Summary of Bayesian binomial GLMMs modeling the direction of submissive chatters among intersexual adult sifaka dyads.

	Model 1a		Model 1b	
Predictor of interest	**Parameter estimate (95% CI)**	**% in ROPE**	**Parameter estimate (95% CI)**	**% in ROPE**
Intercept	7,032.08 (23.33 to 2.73E + 06)	**0%**	963.76 (2.32 to 9.4E + 05)	**0%**
Relatedness (Related)	Inf (0.22 to Inf)	**0.04%**	Inf (0.05 to Inf)	**0.04%**
Parity (Parous successful)	165.56 (11.12 to 3,704.48)	**0%**	192.77 (12.55 to 4,414.50)	**0%**
Parity (Parous unsuccessful)	0.52 (0.10 to 3.31)	12.50%	0.51 (0.09 to 3.03)	12.35%
Reproductive season (Non-mating season)	0.30 (0.08 to 0.96)	**1.69%**	0.51 (0.16 to 1.48)	12.95%
Sex ratio*	0.00 (0.00 to 0.08)	**0%**	0.00 (0.00 to 3.26)	**0.85%**
	N = 1,437		*N* = 1,425	

Exponentiated (odds scale) coefficients and 95% HDI credibility intervals from the regression model are presented. We indicate in bold text those predictors where the % in ROPE value is <5.0% and in italics those predictors with % in ROPE values between 5 and 10%. We considered predictors with % in ROPE values of <10% as potentially important explanatory variables. "Inf" reflects estimates or credibility interval bounds where the odds ratio exceeds 10 billion to 1.

**Sex ratios were calculated at the population level for (a) models and at the group level for (b) models.*

Male Winner vs. Female Winner or Neutral Outcome

In the model including population sex ratio as a fixed effect with the female-initiated subset of data (Model 2a – females), relatedness, female parity status, and sex ratio were potentially important predictors of whether the male won the interaction, but reproductive season was not (**Table 2** and **Figure 3**). While the odds that a male won were much greater when the female was a close relative, relatedness results should be interpreted with caution because we had very few related dyads. The odds that a male won were lower when the female was parous (successful or unsuccessful) as compared to nulliparous and decreased as the population sex ratio became more female-biased. For the same model including population sex ratio as a fixed effect but using the male-initiated subset of data (Model 2a – males), the results were rather different. Relatedness, female parity status, reproductive season, and sex ratio were potentially important predictors of whether the male won the interaction (**Table 2** and **Figure 3**). The odds that a male won were greater when the female was parous unsuccessful (compared with nulliparous) and increased (rather than decreased) as the population sex ratio became more female-biased. The odds that a male won were lower when the female was a close relative (in contrast to the direction of the effect when females initiated the conflict), were lower when the female was parous successful (as compared to nulliparous), and outside of the mating season (**Supplementary Table 1**).

In the model including group sex ratio with the female-initiated subset of data (Model 2b – females), relatedness, female parity, and sex ratio were potentially important predictors of whether the male won the interaction but reproductive season was not (**Table 2** and **Figure 4**). The odds that a male won were greater if the female was a close relative but we had few related dyads in our dataset. The odds that a male won were lower when the female was parous (successful or unsuccessful) compared to nulliparous and decreased as the group sex ratio became more female-biased. In the same model including group sex ratio, but using the male-initiated subset of data (Model 2b – males), relatedness, female parity, reproductive season, and sex ratio were predictors of whether the male won the interaction (**Table 2** and **Figure 4**). The odds that the male won were greater when the female was parous unsuccessful (compared to nulliparous) and increased as the group sex ratio became more female-biased. The odds that a male won were lower when the female was a close relative, when the female was parous successful (compared to nulliparous), and when the conflict occurred outside of the mating season (**Supplementary Table 1**).

Male Winner vs. Female Winner

We next excluded neutral outcomes and only examined conflicts with a "winner" to explore predictors of whether the male won or not. In the model including population sex ratio with the female-initiated subset of data (Model 3a – females), relatedness, female parity status, reproductive season, and sex ratio were potentially important predictors (**Table 3** and **Figure 5**). The odds that the male won were higher when the female was a close relative and increased as the population sex ratio became more female-biased. The odds that a male won were lower when the female was parous (successful or unsuccessful) compared with nulliparous and when the conflict occurred outside of the mating season. In the same model including population sex ratio, but looking at the male-initiated subset of data (Model 3a – males), female parity status, reproductive season, and sex ratio were potentially important predictors (**Table 4** and **Figure 5**). As noted above, relatedness was excluded as a predictor in this model because we observed no cases of males initiating and winning an interaction against a female relative, likely due, in part, to the small number of related dyads in our sample. The odds that the male won were higher when the female was parous (successful or unsuccessful) compared with nulliparous and increased as the population sex ratio became more female-biased. The odds that a male won were lower when the conflict occurred outside of the mating season (**Supplementary Table 1**).

In the model including group sex ratio with the female-initiated subset of data (Model 3b – females), relatedness, female parity status, reproductive season, and sex ratio were important predictors (**Table 3** and **Figure 6**). The odds that the male won were higher when the female was a close relative and increased as the group sex ratio became more female-biased. The odds that a male won were lower when the female was parous (successful or unsuccessful) compared with nulliparous and when the conflict occurred outside of the mating season. In the model including group sex

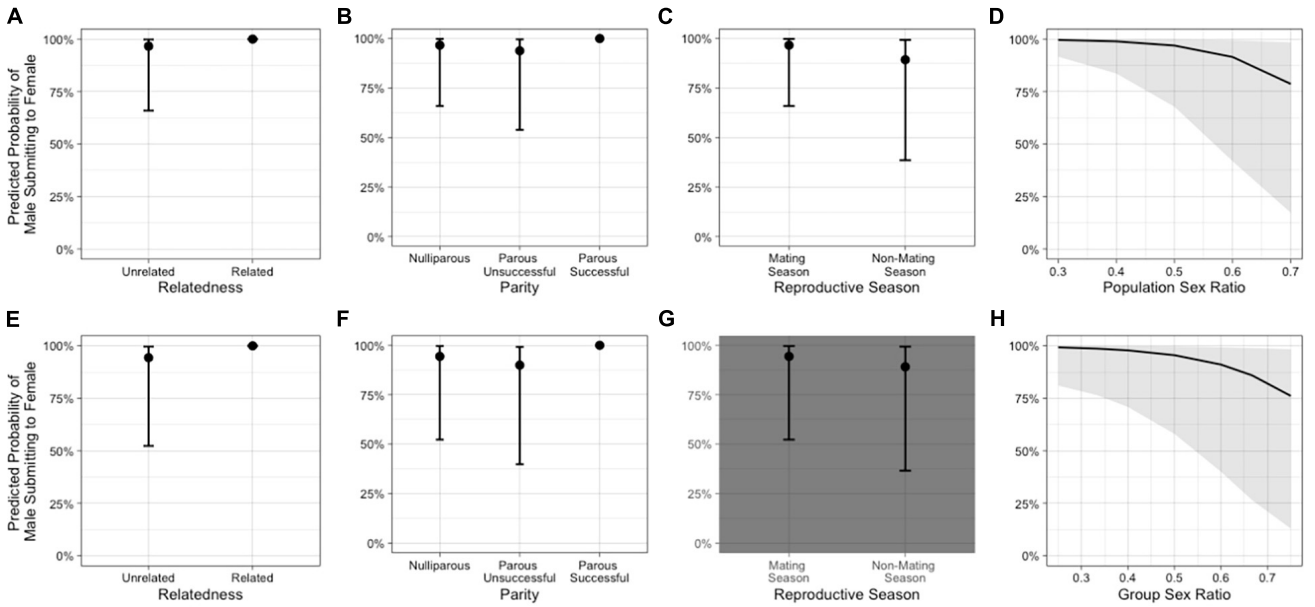

FIGURE 2 | Illustration of the predicted probability of a male submissively chattering to a female based on **(A)** relatedness ($N_{Related}$ = 2 dyads, $N_{Unrelated}$ = 37 dyads), **(B)** female parity, **(C)** reproductive season, and **(D)** population sex ratio for Model 1a, which included population sex ratio as a fixed effect, and based on **(E)** relatedness ($N_{Related}$ = 2 dyads, $N_{Unrelated}$ = 37 dyads), **(F)** female parity, **(G)** reproductive season, and **(H)** group sex ratio for Model 1b, which included group sex ratio as a fixed effect. The gray background in a panel indicates that the variable was not an important predictor in the model.

TABLE 2 | Summary of Bayesian binomial GLMMs modeling whether the male in the interaction won the encounter, examining only adult dyads.

	Model 2a				**Model 2b**			
	Female-initiated		**Male-initiated**		**Female-initiated**		**Male-initiated**	
Predictor of interest	**Parameter estimate (95% CI)**	**% in ROPE**	**Parameter estimate (95% CI)**	**% in ROPE**	**Parameter estimate (95% CI)**	**% in ROPE**	**Parameter estimate (95% CI)**	**% in ROPE**
Intercept	9.45 (0.37 to 304.69)	**3.51%**	0.00 (0.00 to 0.0005)	**0%**	6.31 (0.50 to 103.10)	**4.19%**	0.24 (0.00 to 18,599.49)	**3.15%**
Relatedness (Related)	1.98 (0.08 to 52.55)	*8.72%*	0.00 (0.00 to 129.92)	**0.05%**	3.26 (0.13 to 115.79)	*7.10%*	0.00 (0.00 to 1.47)	**0.01%**
Parity (Parous successful)	0.23 (0.04 to 1.00)	**1.91%**	0.16 (0.00 to 42.34)	**4.58%**	0.22 (0.04 to 1.02)	**1.85%**	0.20 (0.00 to 125.30)	**4.67%**
Parity (Parous unsuccessful)	0.40 (0.10 to 1.33)	*7.62%*	1.99 (0.00 to 1,088.77)	*6.10%*	0.43 (0.11 to 1.49)	*9.96%*	2.86 (0.00 to 1,746.72)	*5.30%*
Reproductive season (Non-mating season)	0.86 (0.43 to 1.63)	40.81%	0.17 (0.01 to 1.94)	**3.48%**	0.95 (0.50 to 1.77)	46.62%	0.07 (0.00 to 0.71)	**0%**
Sex ratio*	0.02 (0.00 to 4.50)	**1.87%**	Inf (7.3E + 06 to Inf)	**0.00%**	0.04 (0.00 to 2.04)	**1.90%**	67.41 (0.00 to 1.34E + 09)	**2.05%**
	N = 1,016		*N* = 834		*N* = 1,010		*N* = 825	

The two possible outcomes were that the male won (1) vs. the male did not win (0), which included interactions won by the female or with no clear winner (a neutral outcome). Separate models were run for female-initiated vs. male-initiated conflicts. Exponentiated (odds scale) coefficients. and 95% HDI credibility intervals from the regression model are presented. We indicate in bold text those predictors where the % in ROPE value is <5.0% and in italics those predictors with % in ROPE values between 5 and 10%. We considered predictors with % in ROPE values of <10% as potentially important explanatory variables. "Inf" reflects estimates or credibility interval bounds where the odds ratio exceeds 10 billion to 1.

**Sex ratios were calculated at the population level for (a) models and at the group level for (b) models.*

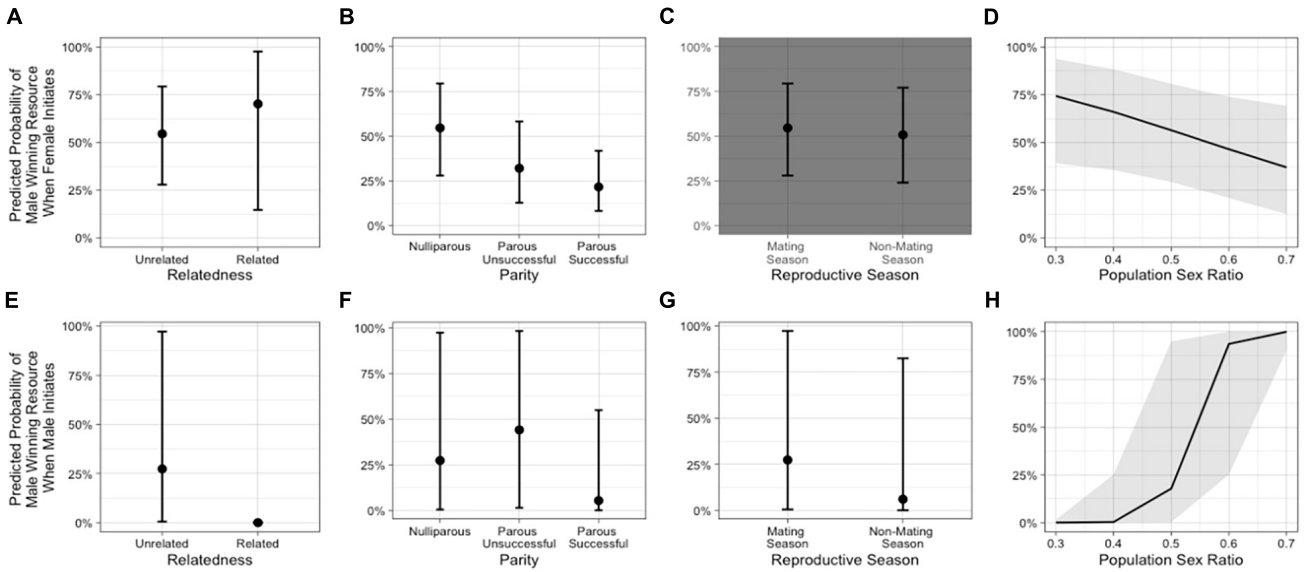

FIGURE 3 | Predicted probabilities from Model 2a of the male in an intersexual agonistic encounter winning a resource (1) vs. the female winning or a neutral outcome (0) when the female initiates the encounter, based on **(A)** relatedness ($N_{Related}$ = 2 dyads, $N_{Unrelated}$ = 39 dyads), **(B)** female parity, **(C)** reproductive season, and **(D)** population sex ratio. The second row depicts the predicted probabilities from Model 2a of the male winning a resource vs. the female winning or a neutral outcome when the male initiates the encounter, based on **(E)** relatedness ($N_{Related}$ = 2 dyads, $N_{Unrelated}$ = 39 dyads), **(F)** female parity, **(G)** reproductive season, and **(H)** group sex ratio. The gray background in a panel indicates that the variable was not an important predictor in the model (see **Supplementary Table 2**).

ratio with the male-initiated subset of data (Model 3b – males), female parity status, reproductive season, and sex ratio were potentially important predictors (**Table 3** and **Figure 6**). The odds that the male won were higher when the female was parous (successful or unsuccessful) compared with nulliparous and increased as the group sex ratio became more female-biased. The odds that a male won were lower when the conflict occurred outside of the mating season (**Supplementary Table 1**).

DISCUSSION

Despite three decades of publications on female economic power (e.g., Hand, 1986; Smuts, 1987; Lewis, 2018, 2020), to date little empirical research has been devoted to examining female leverage over males. We tested the hypothesis that female leverage over males in Verreaux's sifaka varies with the value of the mating opportunity. Adult females rarely chattered submission toward males, but their ability to evoke submission from males was influenced by sex ratio, parity status, and mating season (**Table 4**). Consistent with the hypothesis that economic factors shape female intersexal power, females had more leverage over males when their fertilization potential was higher, there were fewer of them, and they had demonstrated successful mothering skills. Interestingly, the strong unidirectionality (male to female) of submission did not correspond with the direction of wins in intersexual conflicts. Both female losses and neutral outcomes were common (**Figure 1**). Kinship, sex ratio, parity status, and mating season did affect a female's ability to win an intersexual conflict, and mostly as expected. However, female power to win intersexual conflicts was also seemingly determined, in part, by who initiates the agonistic interaction in question. Together, these findings indicate that female leverage varies with the level of commodity value and is conditional. Females have more power over some males than others, and they are able to make males relinquish contested resources in some situations.

Submissive Chatters

Females rarely chattered at males, but the direction of submission in intersexual dyads was influenced by factors that affect the value of a mating opportunity in important ways. Female parity status had a strong effect on submission. Males were >150 times more likely to chatter submissively to a female who had successfully reared an offspring than to a nulliparous female. This finding is consistent with the hypothesis that female intersexual leverage varies with the potential benefits of mating with a particular female. It is likewise similar to earlier research using a different subset of the data from the same population (Voyt et al., 2019) and research on mouse lemurs (*Microcebus murinus*, *M. lehilahytsara*) that found parous females evoke submission from males more than nulliparous females (Hohenbrink et al., 2016). As with other lemurs exhibiting female-biased intersexual power (e.g., Hohenbrink et al., 2016), the potential to reproduce with a female was a less valuable source of leverage outside of the mating season: females were more likely to evoke a submissive chatter from a male during the mating season than outside of it. Additionally, the odds that a male submitted to a female vs. the female submitting to him was lower when the sex ratio was more female-biased, consistent with the idea that female leverage decreases as their

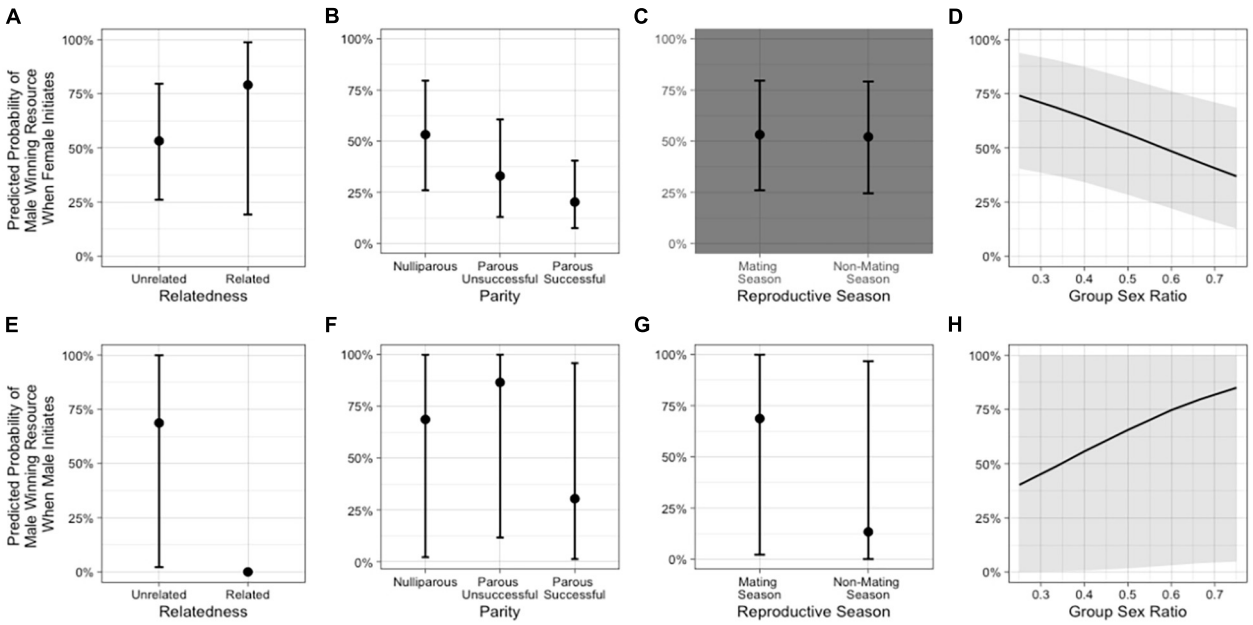

FIGURE 4 | Predicted probabilities from Model 2b of the male in an intersexual agonistic encounter winning a resource (1) vs. the female winning or a neutral outcome (0) when the female initiates the encounter, based on **(A)** relatedness ($N_{Related}$ = 2 dyads, $N_{Unrelated}$ = 39 dyads), **(B)** female parity, **(C)** reproductive season, and **(D)** group sex ratio. The second row depicts the predicted probabilities from Model 2b of the male winning a resource vs. the female winning or a neutral outcome when the male initiates the encounter, based on **(E)** relatedness ($N_{Related}$ = 2 dyads, $N_{Unrelated}$ = 39 dyads), **(F)** female parity, **(G)** reproductive season, and **(H)** group sex ratio. The gray background in a panel indicates that the variable was not an important predictor in the model (see **Supplementary Table 3**).

TABLE 3 | Summary of Bayesian binomial GLMMs modeling whether the male in the interaction won (1) or the female in the interaction won (0) examining adult only dyads.

	Model 3a				**Model 3b**			
	Female-initiated		**Male-initiated**		**Female-initiated**		**Male-initiated**	
Predictor of interest	**Parameter estimate (95% CI)**	**% in ROPE**	**Parameter estimate (95% CI)**	**% in ROPE**	**Parameter estimate (95% CI)**	**% in ROPE**	**Parameter estimate (95% CI)**	**% in ROPE**
Intercept	0.00 (0.00 to 8.05)	**0.59%**	0.00 (0.00 to 3,237.87)	**0.43%**	0.001 (0.00 to 14.19)	**0.91%**	0.24 (0.00 to Inf)	**2.20%**
Relatedness (Related)	19.28 (0.00 to 3.32E + 08)	**2.38%**	NA	NA	14.68 (0.00 to 1.33E + 08)	**2.73%**	NA	NA
Parity (Parous successful)	0.02 (0.00 to 1.72)	**1.22%**	461.11 (0.04 to Inf)	**1.01%**	0.03 (0.00 to 2.24)	**1.33%**	5,759.48 (0.34 to Inf)	**0.31%**
Parity (Parous unsuccessful)	0.31 (0.00 to 40.61)	*6.96%*	5.69E + 07 (1.03 to Inf)	**0.03%**	0.33 (0.00 to 35.87)	*6.94%*	4.35E + 08 (5.79 to Inf)	**0%**
Reproductive season (Non-mating season)	0.18 (0.00 to 2.41)	**4.21%**	0.15 (0.00 to 251.59)	*5.19%*	0.17 (0.00 to 1.77)	**3.08%**	0.08 (0.00 to 74.94)	**3.69%**
Sex ratio*	1,416.75 (0.00 to Inf)	**1.21%**	Inf (0.73 to Inf)	**0.06%**	15.10 (0.00 to 7.97E + 08)	**2.75%**	4.28E + 06 (0.00 to Inf)	**0.56%**
	N = 637		*N* = 327		*N* = 634		*N* = 326	

Separate models were run for female-initiated vs. male-initiated conflicts. Exponentiated (odds scale) coefficients and 95% HDI credibility intervals from the regression model are presented. We indicate in bold text those predictors where the % in ROPE value is <5.0% and in italics those predictors with % in ROPE values between 5 and 10%. We considered predictors with % in ROPE values of <10% as potentially important explanatory variables. "Inf" reflects estimates or credibility interval bounds where the odds ratio exceeds 10 billion to 1.

**Sex ratios were calculated at the population level for (a) models and at the group level for (b) models.*

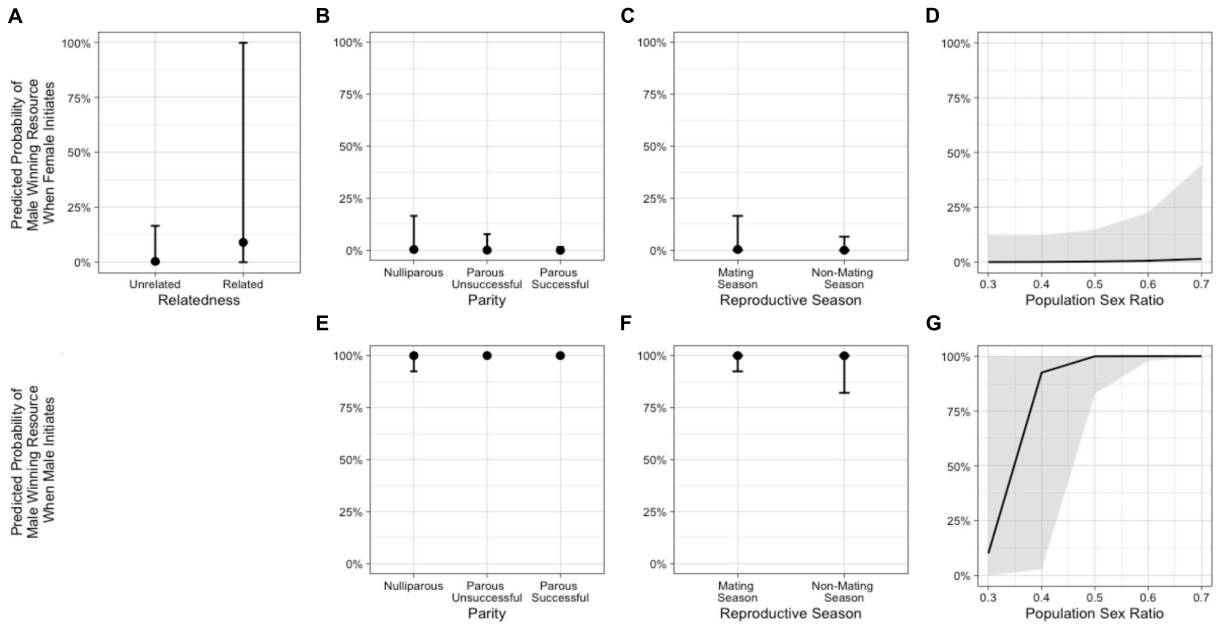

FIGURE 5 | Predicted probabilities from Model 3a of the male in an intersexual agonistic encounter winning a resource (1) vs. the female winning (0) when the female initiates the encounter, based on **(A)** relatedness ($N_{Related}$ = 2 dyads, $N_{Unrelated}$ = 39 dyads), **(B)** female parity, **(C)** reproductive season, and **(D)** population sex ratio. The second row illustrates the predicted probabilities from Model 3a of the male winning a resource vs. the female winning when the male initiates the encounter, based on **(E)** female parity, **(F)** reproductive season, and **(G)** population sex ratio. (See **Supplementary Table 4**).

TABLE 4 | Factors thought to affect the value of mating opportunities with females and pattern of their effects on female leverage in intersexual dyads.

Factor	General pattern of results	What it means for female power
When can a female evoke a submissive chatter from the male?		
When the dyad is related	• Males submit more	• Females have *more* power over males
When the female is parous successful	• Males submit more	• Females have *more* power over males
When it is the mating season	• Males submit more	• Females have *more* power over males
When the population sex ratio is female-biased	• Males submit less	• Females have *less* power over males
When the group sex ratio is female-biased	• Males submit less	• Females have *less* power over males
Does this mean that male also loses the conflict?		
When the dyad is related	• Males win more if females initiate and less in some cases if males initiate	• Females have *less* power over males except when a male initiates a conflict with a related female
When the female is parous successful	• Males win less *except* in some cases if males initiate	• Females have *more* power over males but sometimes male initiation can overcome female power
When the female is parous unsuccessful	• Males win less if females initiate and win more if males initiate	• Female power over males *depends on who initiates the conflict*
When it is the mating season	• Males win more	• Females have *less* power over males
When the population sex ratio is female-biased	• Males win more *except* in some cases if females initiate	• Female have *less* power over males but sometimes female initiation can overcome this reduction in female power
When the group sex ratio is female-biased	• Male winning is variable	• Unclear pattern for female power

We examined the effect of these factors on whether the male relinquishes the resource in two ways: do males win or lose and do males win or not win (lose + neutral outcomes). When combined with initiator effects, this distinction alters the interpretation for female power.

supply increases (Noë et al., 1991; Noë, 2017). Previous primate research has also found that sex ratios can have important effects on female power (Hemelrijk et al., 2008; Izar et al., 2021). Taken together, our results suggest that female power over males is influenced by economic factors: female power to evoke submission from males increases with the increasing

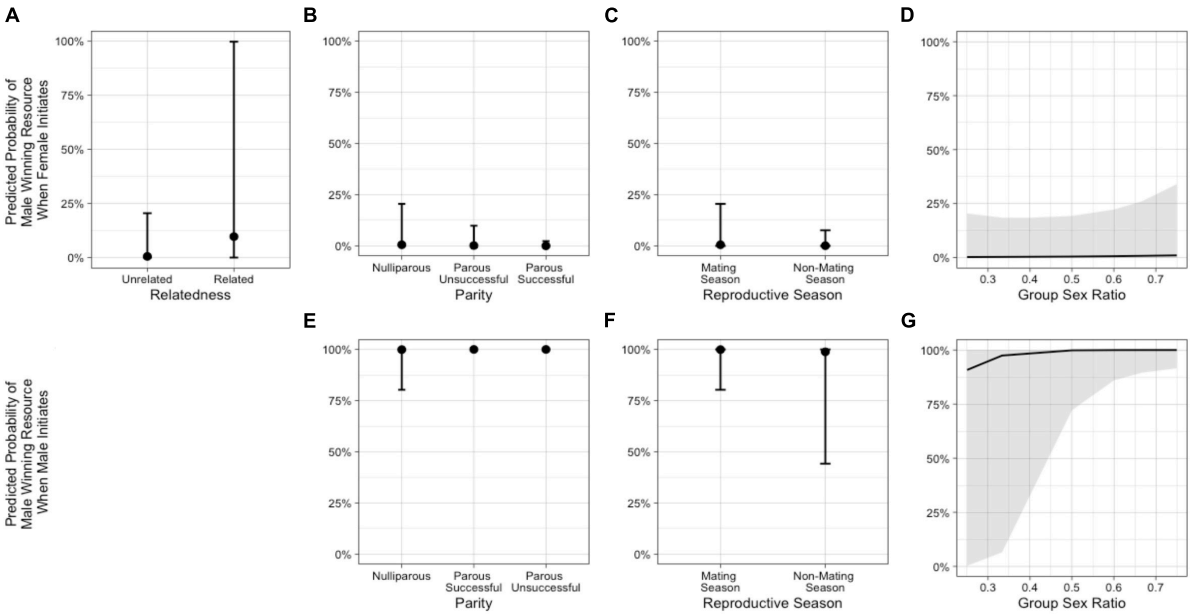

FIGURE 6 | Predicted probabilities from Model 3b of the male in an intersexual agonistic encounter winning a resource (1) vs. the female winning (0) when the female initiates the encounter, based on **(A)** relatedness ($N_{Related}$ = 2 dyads, $N_{Unrelated}$ = 39 dyads), **(B)** female parity, **(C)** reproductive season, and **(D)** group sex ratio. The second row illustrates the predicted probabilities from Model 3b of the male winning a resource vs. the female winning when the male initiates the encounter, based on **(E)** female parity, **(F)** reproductive season, and **(G)** group sex ratio. (See **Supplementary Table 5**).

value of the fertilizable egg and decreases with increasing supply of females.

Contrary to our expectation, however, we did not find that females had greater leverage over unrelated males. Instead, males were more likely to chatter submissively to close female relatives. One possibility is that a different base (*sensu* Lewis, 2002, 2020) of power, i.e., genes, is a stronger determinant of intersexual power than mating opportunities among kin. Kin selection can mask economic effects (Noë et al., 1991) because, like leverage (Hand, 1986), inclusive fitness adds to the cost of winning in some conflicts. Sex differences in the opportunity costs of inbreeding might also influence intersexual leverage if females exhibit a strong preference to avoid inbreeding (Antfolk et al., 2012). While our findings regarding the effects of relatedness on female leverage should be interpreted with caution because we had very few related dyads in our dataset, our analyses of individuals aged $\geq$ 3 years that included $\geq$ 20 related dyads found the same unexpected effect (**Supplementary Table 2**). More research is clearly needed regarding the effect of kinship on intersexual power in sifaka, but our results suggest that female intersexual leverage may not be consistent across all males.

Wins

Our analysis of whether a male wins an intersexual conflict presents a different and more complicated picture of the factors impacting female leverage. While males readily signaled submission to females (**Figure 1**), it was not uncommon for females to use repeated aggression to convince a male to relinquish a resource, irrespective of whether he chattered after each aggressive act. Females also sometimes had to use a combination of aggressive acts (e.g., lunge, cuff, and bite) before eventually winning the encounter. Thus, the power to evoke submission is clearly very different from the power needed to usurp a resource from another individual.

For the most part, economic factors had the predicted influence on female power (**Table 4**), but the sex of the individual that initiated the conflict was an important mitigator. For example, consistent with expectations based on market effects, the odds that a male won a conflict increased as the supply of females increased, but only when males initiated the conflict and only when sex ratio was examined at the population level [(a) models]. Our other results regarding sex ratio effects [i.e., in the group sex ratio (b) models and in population sex ratio models when females initiated the conflict] were inconsistent with expectations based on market effects. Furthermore, reproductive season was not an important determinant of which sex won a conflict unless the male initiated, in which case, contrary to expectations and contrary to the pattern for submissive chatters, males were more likely to win during the mating season. Overall, these findings suggest that economic factors may have some influence on female intersexual power to win agonistic contests, but these affects can be limited.

Our finding that males often are more likely to win when they initiate may be associated with what Flack and de Waal (2007) termed as "subordination signaling" (i.e., when power relationships are fairly institutionalized and individuals spontaneously communicate their lower status to higher ranking groupmates, in contrast with reacting submissively in response to agonism). In a study of power in the different but nearby

Kirindy Forest population of Verreaux's sifaka, Lewis (2019) found that when males emit chatter vocalizations in peaceful contexts (i.e., without provocation), females were less likely to usurp the resource. In our data for the Ankoatsifaka population of sifaka, an interaction could be initiated with an approach, an aggressive act, or an unprovoked submissive act, depending on when the agonistic interaction occurred within a sequence of behaviors (e.g., an approach was only scored as the initiation of the interaction if the agonism began immediately afterward; the approach was not scored as the beginning of the conflict if the dyad members were, for example, in proximity for 20 min prior to the onset of the conflict). Thus, males may be more likely to win an agonistic interaction if they initiated it because (1) they are unlikely to use aggression unless they have a good chance of winning, (2) they may be more likely to win because they started the interaction with an unprovoked, peaceful chatter, or (3) they approached and immediately chattered (cf. "appeasement": Beisner and McCowan, 2014). In other words, when males start an agonistic interaction by signaling "subordination" (i.e., communicating their lower status without provocation: Flack and de Waal, 2007), they may be more likely to "win." By providing more information, communication can increase the chance of a peaceful resolution to conflicts (Noë et al., 1991). Given the seemingly importance of initiator sex for determining who wins an intersexual conflict, further research is needed to explore the causes and consequences of different strategies for initiating interactions.

Neutral Outcomes

One of the most surprising results of this study is the finding that half of sifaka agonistic encounters end with both individuals sitting beside one another rather than a withdrawal by one of the interactants. A central dogma of ethology is that winners gain or maintain possession of a resource while losers retreat and avoid further escalation (Parker, 1974). Despite this focus on the binary results of winning and losing, sharing or tolerance is a third possible outcome (Hall et al., 2020). Communication of lower status in the relationship reduces usurpation of resources in sifaka (Lewis, 2019) and may similarly increase the chance that a higher-ranking individual will share a resource. Indeed, sifaka negotiate their relationships using a variety of behaviors (e.g., Lewis, 2005). While it is possible that our operational definition measured in seconds rather than in minutes may partially explain the large number of interactions scored as neutral, the vast majority of outcomes would have been scored the same regardless. Moreover, the speed with which a loser withdraws from a conflict should be indicative of a winner's power. Supplants involve an immediate displacement of another individual, and exploration of our data indicated that our results did not differ much whether we included (as we do here) or excluded supplants from the dataset. Our study suggests that examining neutral outcomes in more detail may be a fruitful area of future research.

Not all Outcomes Are Equal

Our study also demonstrates the importance of examining multiple scopes of power (*sensu* Lewis, 2002, 2020) within the full landscape of power (Lewis, 2022). The consequences of female intersexual leverage in sifaka include both evoking submissive chatters and winning resources from males. As noted above, and unlike some other species with female-biased intersexual power (e.g., wooly lemurs: Ramanankirahina et al., 2011) however, female sifaka abilities to achieve these outcomes are not the same. Sifaka chatter vocalizations are formalized signals (Kraus et al., 1999; Lewis, 2019), and, as such, they unambiguously communicate status (de Waal, 1986). These kinds of signals are argued to be associated with a stable layer of power while winning is associated with a more flexible layer of power (e.g., "structure" vs. "surface structure": Hinde, 1979; "formal dominance" vs. "real dominance": de Waal, 1986). Hence, when a conflict arises, a male may be able to evoke a win or a neutral outcome with a female if he signals with a chatter vocalization that the stable layer of power is unchanged. Our results are consistent with the hypothesis that a male's communicating about formal status (de Waal, 1986; cf. "structural power": Hinde, 1979; cf. "relationship state": Flack and de Waal, 2007) reduces the chance that a female will usurp contested resources, as was suggested by previous research on a different population of Verreaux's sifaka (Lewis, 2019). Our study also highlights the value of investigating multiple scopes of power within the same study.

Evolutionary Explanations of Female-Biased Power

Hypotheses about the evolution of female-biased power often point to the importance of resources for female fitness, such as explanations centered around the energetic constraints that females face for supporting reproduction (e.g., Jolly, 1984; Young et al., 1990; Wright, 1999). Researchers then often test these hypotheses by recording whether interactions are "decided" or "undecided" based upon whether one individual exhibits submissive behaviors (Pereira et al., 1990; Pereira and Kappeler, 1997; Pereira, 2006). The implicit assumption in these studies is that if a female can evoke submission from a male, then she wins the interaction. Our study, however, demonstrates that signaling submission and winning access to a resource are not the same. Sifaka males often chatter submissively to a female, but then do not relinquish a resource to her (neutral outcome). Likewise, females also often abandon a resource after the male communicates his subordinate status (Lewis, 2019), effectively the male "wins." If food and other resources are so critically important to female fitness that it drives the evolution of female-biased power structures, then one would expect intersexual conflicts to result in females more consistently usurping or maintaining control of those resources, but our results suggest that this is not the case, at least among sifaka. Female power in intersexual relationships is known to incorporate a variety of behaviors and outcomes, including aggression, submission, and priority of access to resources (Kappeler, 1990; Radespiel and Zimmermann, 2001; Lewis, 2018, 2020). More research into how these behaviors and outcomes relate with one another is needed if the evolutionary causes of female-biased power are to be determined.

CONCLUSION

Biological markets result in power asymmetries (Noë et al., 1991; Noë and Hammerstein, 1994, 1995; Lewis, 2002; Noë, 2017). Voyt et al. (2019) demonstrated that female intersexual power in Verreaux's sifaka is better described as "female leverage" than "female dominance" because females seem to derive power from their control over a resource in high demand – namely an egg that can be fertilized to produce offspring – rather than an asymmetry in fighting ability. Our study builds on this previous research by demonstrating that economic factors affecting the value and supply of reproductive opportunities influence female leverage. The value of mating opportunities is greater when the female has successfully demonstrated that she can translate fertilization into surviving offspring (and presumably higher fitness) and can be discounted outside of the mating season, when the fertilization opportunity that a female represents may not be available for months. However, we also found that factors other than market effects, such as who initiates a conflict, can impact who wins the resource, if anyone wins at all. Finally, our finding that males are less submissive to close female kin highlights the value in conceptualizing the phenomenon often referred to as "female dominance" as an aggregate of multiple social relationships. Rather than all females having power over all males, this power can vary across and within dyads, as well as over time and between contexts. Greater attention needs to be placed on understanding female leverage and this relational aspect of power. The "power framework" (Lewis, 2002, 2020) provides useful tools for standardizing this endeavor. Power is multi-faceted, and more studies will be needed to understand the full power landscape (Lewis, 2002, 2020) in Verreaux's sifaka and other animals exhibiting female-biased power.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.org/10.5061/dryad.ngf1vhhwh.

ETHICS STATEMENT

The animal study was reviewed and approved by University of Texas at Austin Institutional Animal Care and Use Committee and the CAFF/CORE Committee in Madagascar.

AUTHOR CONTRIBUTIONS

RL conceived the study, collected the data and paid the research assistants. RL and AD funded for the project. RL and GB scored the data. GB and AD analyzed the data. All authors designed the study, wrote and edited the manuscript.

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Dynamics of intersexual dominance in a highly dimorphic primate

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Intersexual dominance, which is measured by the probability that members of one sex elicit submission of members of the other sex during agonistic interactions, is often skewed in favor of males. However, even in sexually dimorphic species, several factors may influence intersexual dominance. Here, we use an 8-year dataset to examine the dynamics of intersexual dominance in wild-living mandrills (*Mandrillus sphinx*). Mandrills exhibit an extreme male-biased sexual size dimorphism but females show pronounced kin-differentiated social relationships and occasionally form coalitions against males. We established intersexual hierarchies across consecutive 6-month time blocks, representing either mating or birth seasons. Although females appeared to outrank 11% of males, they elicited male submission in only 2% of agonistic interactions against males. This discrepancy is likely due to the temporary residency of most males in the exceptionally large mandrill groups, the sexually coercive male mating strategies and the scarce number of agonistic interactions within most dyads, that may limit hierarchical inferences. In a second step, we found that the intersexual hierarchy mixes the intrasexual ones respecting their respective order. Females outranked mostly young and old males during the mating (vs. birth) season and social integration was positively correlated to dominance status in both sexes. In a third step, we found that females win more conflicts against young or old males which are closer to them in the intersexual hierarchy. These results extend our understanding of female-male dominance relationships by indicating that female mandrills occasionally outrank males who are considerably larger than them, and that a combination of demographic and social factors can influence the intersexual hierarchy.

KEYWORDS

intersexual dominance, hierarchy, agonistic interactions, social bonds, mandrills

1. Introduction

Intersexual hierarchies reflect sexual asymmetries in the outcome of agonistic interactions, which are often biased toward males. Despite their importance for the social structure, mating strategies and life-history of a species (Parker, 2006), studies of dominance hierarchies have long been restricted to intrasexual contexts

(Ellis, 1995; Davidian et al., 2022), sometimes considering by default that all males are dominant over all females (Lewis, 2018). However, recent studies that have quantified intersexual dominance *via* the construction of intersexual hierarchies draw a more nuanced and dynamic landscape (Lewis, 2020; Davidian et al., 2022; Kappeler et al., 2022), where intersexual dominance varies along a continuum, including more balanced female-male dominance relationships (e.g., Hemelrijk et al., 2020). Except for a handful of well-known species with female-biased dominance [bonobos (*Pan paniscus*): Parish et al., 2000; most lemurs: Kappeler, 1993; Petty and Drea, 2015; spotted hyenas (*Crocuta crocuta*): Kruuk, 1972], there is a growing list of species with circumstantial or contextual female dominance over males (primates: Dunham, 2008; Hemelrijk et al., 2008; Ferrari, 2009; Izar et al., 2021; small mammals: Murie and Harris, 1988; Koren et al., 2006; Hewitt et al., 2009; birds: Smith, 1982; Jawor, 2000; see also Hand, 1986).

Our understanding of why intersexual dominance is biased toward females in some species, and toward males in others is still fragmentary and often relies on taxon-specific hypotheses (Kappeler and Fichtel, 2015; Lewis, 2018; Davidian et al., 2022). In addition, there are still several sources of uncertainty concerning the structural properties of intersexual dominance hierarchies. First, it has long been unclear whether intrasexual dominance rank predicts intersexual rank because intrasexual agonistic interactions may target different resources and dominance relationships may be established and maintained through different mechanisms depending on the sex (e.g., inherited vs. fight-based hierarchies; Clutton-Brock and Huchard, 2013b; Tibbetts et al., 2022). A recent analysis including several mammal species indicates, however, that the rank order of same-sex individuals is often conserved in intersexual hierarchies (Kappeler et al., 2022). Second, dominance hierarchies based on matrices constructed with different methods can lead to different results (Lewis, 2002). Agonistic interactions may have different forms and variable outcomes. Although standardized methods to quantify intersexual dominance have been recently proposed (Kappeler et al., 2022), previous studies often mix, for example "undecided" (i.e., not systematically followed by submissive behaviors) and "decided" interactions or even aggressive and submissive behaviors (e.g., Hemelrijk et al., 2020) to construct dominance hierarchies which may affect the comparability of results. Aggression is often expressed under tensed circumstances during social conflicts while submission is regularly, and often spontaneously, expressed in ritualized contexts outside situations of social tension, and may constitute more reliable cues of perceived dominance relationships (Kappeler et al., 2022). Additionally, in species with dominance biased toward males, females may threaten or direct aggression toward males during conflicts or tensed situations when they are aroused, while they may be unable to elicit male submission in routine situations (French et al., 2013). In contrast, in Verreaux sifakas (*Propithecus verreauxi*) where females are strictly dominant over males, nearly 90% of spontaneous submissions are expressed by males toward females, while females win only about 1/3 of intersexual conflicts (Lewis et al., 2022). Overall, females may appear more or less dominant over males in social hierarchies built using different types of social interactions.

Apart from aggressiveness or physical characteristics (e.g., size or strength), demographic and ecological factors may also influence the dynamics of intersexual dominance hierarchies within groups or populations (Chase et al., 2002; Lewis, 2002; Hewitt et al., 2009; Young et al., 2017; Hemelrijk et al., 2020). First, the group sex-ratio influences the intersexual dominance and females outrank more males when the number of males in the group increases (Hemelrijk et al., 2020; Lewis, 2020; Izar et al., 2021). In primates, female dominance over males may emerge from the so-called "winner and loser effects" where more males in a group fight more, causing more losses and injuries in subordinate males who may eventually submit to females (Hemelrijk et al., 2008; but see also Bonabeau, 1999). Alternatively, this effect may reflect the dynamics of "mating markets" (Noë and Hammerstein, 1994; Gumert, 2007), where fluctuating sex-ratios affect the relative sex-based leverage gained by fertile females, as the relative value of fertilizable eggs increases with their rarity, i.e., when there are less fertile females for a larger number of males. Therefore, females who control the access to their eggs—a valuable resource for males that cannot be taken by force—(Lewis, 2002, 2018, 2020) may have increased intersexual dominance as males might be more cooperative or compliant in order to gain access to fertile females. Accordingly, females may be more or less dominant depending on their reproductive state: for example, female mouse lemurs win more intersexual conflicts during the reproductive season than outside of it (Hohenbrink et al., 2016), and in many monogamous birds, females are more dominant over males when they are sexually receptive (Smith, 1980). Finally, social support and coalitions can also influence the outcome of agonistic interactions in different taxa (Weiß and Kotrschal, 2004; Markham et al., 2015), and may shape emerging hierarchies and reinforce established ones (Bissonnette et al., 2009; Strauss and Holekamp, 2019; Vullioud et al., 2019). In mammals, female philopatry is frequent (Greenwood, 1980), and philopatric females often ground their dominance relationships on social support (Clutton-Brock and Huchard, 2013a), which may further influence the outcome of intersexual interactions, as shown in spotted hyenas (Vullioud et al., 2019). However, few studies have examined the influence of social support on intersexual dominance in species where males are generally dominant over females. Overall, while new evidence indicates that intersexual dominance can be flexible and context-dependent, we know little regarding the extent and determinants of such variation, i.e., the ecology of intersexual dominance.

In this study, we investigate intersexual dominance relationships in mandrills (*Mandrillus sphinx*). Mandrills are

primates of the *Cercopithecidae* family living in polygynandrous groups including hundreds of individuals (Abernethy et al., 2002). They are seasonal breeders and most males enter the group at the onset of the mating season and leave afterwards, with only a few males remaining in the group during the birth season (Brockmeyer et al., 2015). Male-male competition is severe in this species (Setchell, 2016) and results in high reproductive skew, with 60–70% of reproductions monopolized by the alpha male (Charpentier et al., 2005, 2020). Mandrills exhibit extreme sexual size dimorphism: males are on average 3.4 times heavier than females (Setchell et al., 2001) while they display upper canines almost 5 times longer than females (Leigh et al., 2008). Male mandrills attain adult size and mass and show a major increase in mounts of fully swollen females (likely to be fertile) around the age of 9–10 years (Setchell et al., 2001). Their dominance rank increases with age, peaks from 11 to 16 and falls again after 16 years (Setchell et al., 2006b). Adult males are sexually coercive (Smit et al., 2022) and mate-guard females when they display maximally turgescent sexual swellings around ovulation (Setchell et al., 2005a). Females are philopatric and form differentiated social bonds and linear matrilineal hierarchies, with maternally inherited ranks that are relatively stable across their lives (Setchell et al., 2002). Despite the large physical asymmetries between sexes in mandrills, females can form coalitions against males, sometimes exceptionally violent (Setchell et al., 2006a).

In a first step, we investigate the dynamics of intersexual dominance in mandrills at the "population level," indexed by the percentage of males outranked by an average female in consecutive 6-month time blocks over an 8-year study period. We build intersexual dominance matrices using only dyadic decided interactions (i.e., when one opponent exhibited submission) and we compute dominance hierarchies based on (i) all submissive behaviors (whether or not they follow aggression) and (ii) ritualized submissive behaviors only (in the absence of aggression), to test if intersexual dominance varies across behavioral contexts. We predict females to outrank less males when the social hierarchy is based on ritualized submissive interactions only, compared to a dataset comprising aggressive interactions occurring during aggressive encounters. In a second step, we investigate factors that could influence the probability that a given female outranks a given male. We expect that (i) intrasexual dominance rank position predicts the position of an individual in the intersexual hierarchy, (ii) females outrank more males during the mating season, when they are sexually receptive and thus have more leverage, and when the group includes more males. We further expect that (iii) more socially integrated individuals are more dominant over the other sex as they have more social support, and that (iv) females have a higher probability to outrank males who are not in their prime (the age range when males are the strongest). In a final step, we investigate factors that may influence the probability of a female to win an intersexual conflict. We predict that (i) the greater the rank difference between the opponents (i.e., the more dominant the male and the more subordinate the female) the lower the probability for the female to win, (ii) sexually receptive females win more conflicts than females in other reproductive states, given that they have more sex-related leverage, and (iii) females have a higher probability to win conflicts against males who are not in their prime.

2. Materials and methods

2.1. Study system

We studied a natural population of mandrills living in a private park located in Southern Gabon. The population was established in 2002 after the release of 36 captive individuals initially housed in CIRMF (Centre International de Recherches Médicales de Franceville, Gabon). Another 29 individuals were released in 2006 (Peignot et al., 2008; Charpentier et al., 2020). Wild male mandrills were observed to join the group to reproduce, starting in 2003. A field research project (Mandrillus Project) was set-up in early 2012 to monitor the ecology, life-history and behavior of the population. Only 6 adult females out of 230 individuals (from which 79 were adult females) of the group were captive-born in late 2021. All the individuals of the population are individually recognized and daily censused.

We used behavioral, demographic and life-history data collected from April 2013 to September 2021 on 93 adult females (aged 4 years and older) and 35 subadult and adult males (aged 9 years and older). We included subadult males (aged 9–10 years) because males at this stage are fully-grown and have usually entered the male-male competition and started mating with females (Setchell and Dixson, 2002; Setchell et al., 2005b). When the exact birth date was not known or approximated to a few days, we estimated it using body condition and patterns of tooth eruption and wear (Galbany et al., 2014).

We divided the study period in 6-month time blocks roughly equating to the mating (April-September) and birth (October-March) seasons (Dezeure et al., 2022). When an individual turned adult during a season (6-month time block), we included it for the whole season.

We calculated a monthly group sex ratio (SR) as the number of adult females present in the group divided by the number of subadult and adult males that were censused in the group that month for at least a day. We also calculated the mean SR of each 6-month time block. Because the number of males largely varies between the mating vs. the birth season, season (birth vs. mating) and group sex-ratio are correlated (Spearman's rank correlation: rho = 0.59, $p = 0.02$) and we thus used these two effects in alternative models.

2.2. Behavioral data

2.2.1. Behavioral sampling

Behavioral observations were made by observers blind to the focus of this study. We considered only dyadic interactions between adult females and adult or subadult males. *Ad libitum* observations and 5-min focal sampling (Altmann, 1974) were performed daily by recording, *inter alia*, affiliative and agonistic interactions between group members. In this study, we used four submissive behaviors: (i) "avoidance": when an individual A walks away from an individual B who is approaching, (ii) "displacement": when A walks away from B and B takes the place of A, (iii) "escape": when A flees away from B who expresses aggression and (iv) "submissive vocalization": when A emits a typical submissive vocalization after B expresses aggression. We calculated intra- and intersexual hierarchies based on two different datasets: a "full dataset" that comprised all submissive interactions (which were preceded by an aggressive event, or not) and a "ritualized dataset" that included only submissive interactions that were not preceded by an aggressive event. These two datasets allowed to test for potential discrepancies in dominance hierarchies due to methodological differences. We, however, did not use "undecided" aggressive interactions, i.e., those that were not followed by a submissive event, and which may not capture intersexual dominance relationships accurately.

2.2.2. Behavioral dataset

We considered a total of 2,768 h (40,678 focal observations) of focal data in addition to *ad libitum* observations. For the analyses based on the full dataset, we used interactions from both focal and *ad libitum* observations to increase our sample size. In the ritualized dataset, we used only interactions from focal observations to filter out submissive behavior that followed an aggressive event. In the linear regression models performed below, we used only the full dataset given the similarity of the results based on these two different datasets (see results). For the analysis of intersexual conflicts, we selected from the full dataset all the dyadic interactions between an adult female and an adult male, recorded during focal observations, for which the outcome was unambiguous, i.e., when only one of the two individuals exhibited an aggression (mild threats were not included) followed by a submission from the other individual.

2.2.3. Dominance hierarchies

We used the functions *DS* and *ISIranks* from the R package *EloRating* (Neumann et al., 2011) to compute the intersexual hierarchies with both normalized David's score (David, 1987) and I&SI (de Vries, 1998) to evaluate whether these two rank estimates yielded different results suggesting potential methodological biases. David's score is calculated for each individual based on the observed dyadic proportions of wins. Namely, the number of dyadic wins (where the opponent submits to the focal individual) is divided by the sum of dyadic wins and losses (where the focal individual submits to the opponent) over other groupmates (for a formal definition, see David, 1987). As such, the difference among two individuals' scores is more informative than the difference between their ordinal ranks, and reflects the extent of asymmetry in dominance-based power between these individuals. We used normalized David's scores because they correct for the possibility that the observed outcomes occur by chance. Such a possibility is calculated on the basis of a binomial distribution with each animal having an equal chance of winning or losing each agonistic interaction (de Vries et al., 2006). This correction is crucial when the number of interactions greatly differs among dyads, like in our study group. However, David's score may be sensitive to missing data (non-interacting dyads; Neumann et al., 2011). Indeed, in our dataset, almost two out of three (62 $\pm$ 15%; $\pm$SD) intersexual dyads never interacted agonistically, on average, while this figure was 32 $\pm$ 17 and 71 $\pm$ 10%, respectively, in male-male and female-female dyads (Supplementary Table S1). Consequently, intrasexual agonistic interactions may be highly influential in inference of intersexual hierarchies. To evaluate this possibility, we built intersexual hierarchies based on (1) intra- and intersexual agonistic interactions, and (2) intersexual interactions only. Second, we also used I&SI, another dominance index that generates the most parsimonious ordinal rank (the ordinal rank that deviates the least from linearity) based on multiple randomizations (N = 500) that re-order individual ranks from an interaction matrix (de Vries, 1998). Due to this iterative process, the resulting order may include more than one "solution" in the form of several equally likely rank orders. Whenever needed, we averaged the rank of each individual across these equally likely solutions (as per Kappeler et al., 2022). Finally, due to the randomization process, whenever we re-ran the algorithm, the resulting hierarchy could be slightly different (Supplementary Figure S1B). Due to the high level of correlation between David's scores and I&SI within (see results) and across species (Kappeler et al., 2022) and the greater stability of hierarchies based on David's scores (Sánchez-Tójar et al., 2018), we used normalized David's scores (David, 1987) for downstream analyses. In order to examine the robustness of the resulting intersexual hierarchy, we also used two randomization tests which are described in the Supplementary Figure S1. The number of individuals, the interactions among them and the percentage of interacting dyads (over all the possible dyads) are also shown in Supplementary Table S1.

2.2.4. Social integration and affiliation rates

During focal samplings, grooming events and their duration were recorded. For each 6-month time block, we used the total time of grooming recorded among females to

create a female-only grooming directed network (function *graph_from_data_frame* from the package *igraph*; Csardi and Nepusz, 2006). We calculated the in-degree of each female from the above networks, as a proxy of social integration and support. We used only the number of females grooming (and not groomed by) a female, because we consider these individuals more likely to offer their support during agonistic interactions. Similarly, we calculated the total (in and out) degree of each male in networks including only intersexual grooming interactions (number of females grooming or being groomed by each male). For males, we considered all (given and received) grooming interactions in order to capture better male integration with the females of the group, rather than female support to males.

2.2.5. Reproductive state

The reproductive state of each adult female was determined on a near-daily basis based on sexual swelling size (scaled from 0 to 3 by increments of 0.5) and patterns of gestation and lactation. During an estrous cycle of a female mandrill, the perineal swelling inflates for some days and reaches maximal swelling size around ovulation where it remains maximal for a few days before deflating. Each female was classified as: "non-swollen" (i.e., in the non-fertile phase of the cycle that does not fall within the following three categories), "swollen" (i.e., exhibiting an inflating or maximal perineal sexual swelling), "pregnant" (i.e., exhibiting a characteristic pregnancy swelling and/or if the female gave birth less than 163–190 days after a given day; average gestation length: mean ±SD: 175.0 ± 4.7 days; Dezeure et al., 2022) or "lactating" (i.e., nursing a ≤6 month-old infant, without having resumed cycling).

2.3. Statistical analyses

First, at the level of the population, we ran a Spearman's rank correlation test to study whether the intersexual hierarchy differed when using either David's score or I&SI. We then compared the percentage of males dominated by an average female in the two datasets (including all submissive interactions vs. only ritualized submissive interactions) using a Spearman's rank correlation test.

Second, at the dyad level, we ran a generalized linear model (GLMM) with a binomial distribution and a logit function to test whether the probability of a given female to outrank a given male was influenced by the following fixed factors: female and male intrasexual ranks and ages, female's in-degree in the female-only social network and its corresponding quadratic term (suggested following a graphical exploration of the data), and male's total (in and out) degree in the social network including only intersexual grooming interactions and either season or sex ratio. Female, male and dyad identity and the year were fitted as random factors.

Third, at the interaction (conflict) level, we ran a GLMM with a binomial distribution and a logit function to test whether the probability to unambiguously (only one of the two individuals exhibits aggression followed by a submission from the other individual) win an intersexual conflict (1/0; response variable) for a given female was influenced by the following fixed factors: the rank difference between opponents (male and female David's scores in the intersexual hierarchy), the age of the female, the age of the male and the corresponding quadratic term, and female's reproductive state. The female, male and dyad identity and the year were fitted as random factors.

We ran the above tests and models in R version 4.0.3 with the functions *cor.test* of the package *stats* and *glmmTMB* from the package *glmmTMB* (Magnusson et al., 2017). We used the *Anova* function of the package *car* (Fox et al., 2009) to test the significance of all fixed factors and we computed their 95% confidence intervals. We used the performed correlation tests to detect potential multicollinearities and we validated the performed models using the package *DHARMa* (Hartig and Lohse, 2020).

3. Results

3.1. Metrics of dominance hierarchy and robustness tests

Female mandrills elicited male submissive behaviors in 2.4 ± 2.1% (±SD) of intersexual agonistic interactions. However, we found that females can outrank males, with a female outranking, on average, 11.3 ± 6.2 % (±SD) of males (results based on the full dataset and David's score or 18.2 ± 8.1% based on I&SI). We found a positive correlation between David's score and I&SI metrics across 6-month time blocks (Spearman's rank correlation, rho = 0.53, p = 0.03; see also Kappeler et al., 2022). When we calculated the hierarchy 500 times using David's score, each time randomly selecting 50% of all agonistic interactions, an average female outranked 12.1 ± 0.8% (mean ± SD) of males (Supplementary Figure S1A). When we calculated the hierarchy 500 times using I&SI, we found that no iteration resulted in an intersexual hierarchy where all females are outranked by all males and an average female outranked 16.1 ± 1.5% (mean ± SD) of males (Supplementary Figure S1B) across all iterations.

When we calculated the intersexual hierarchy using only intersexual agonistic interactions, the percentage of males outranked by an average female was similar to the percentage resulting from the calculation of the hierarchy with both intra- and intersexual agonistic interactions (11.5 ± 6.0 %; results based on David's score). Additionally, we found a strong positive correlation between the average number of males dominated by a female when using all submissive interactions and when using only ritualized submissive interactions (Spearman's rank correlation, rho = 0.72, p = 0.001 when we used David's score).

When we used only ritualized submissive interactions to build the intersexual hierarchy, a female appeared to outrank, on average, 9.3 ± 5.1% (±SD; results based on David's score; see previous paragraph for the results based on the full dataset) of males.

Despite these congruent hierarchies resulting from various metrics and datasets, the discrepancy between the percentage of intersexual interactions where a male showed submission toward a female and the percentage of males dominated by an average female appears puzzling. In addition, in 92.7 ± 6.0% of female-dominant intersexual dyads, the two individuals never interacted agonistically, while in male-dominant dyads the corresponding percentage was 60.3 ± 14.4%. From a total of 5,433 intersexual dyads, only 1,844 interacted agonistically at least once, including 1,805 male-dominant dyads and only 39 female-dominant dyads. In these 39 dyads, males showed submission, on average, in 18.8 ± 3.8% of the interactions while in male-dominant dyads, males showed submission in 2.3 ± 12.9% of the interactions.

3.2. Trait and social influences on intersexual hierarchies

A given female had a significantly higher probability to outrank a male when she was high-ranking and when he was low-ranking, in comparison to any other combination of rank-sex class (Figure 1A and Table 1). The probability for a female to outrank a male was significantly higher when male degree (number of female grooming partners) was lower (Figure 1B) and female in-degree (number of female partners grooming her) was higher although this relationship was not linear (Figure 1B and Table 1), suggesting that females need at least a certain number of female partners in order to have higher chances to outrank a male. In addition, a female had a higher probability to outrank a male during the mating (than birth) season (Table 1) or when the group sex ratio was male-biased (i.e., when there were more males in relation to females in the group; Chisq = 18.687, $p < 0.001$). Female age was not significant but a female had a higher probability to outrank younger and older males than males in their prime (Figure 2 and Table 1).

The probability for a given female to win a conflict (only 11 out of 382 intersexual conflicts were won by females) against a given male was higher for younger males than for males in their prime and tended to increase again when the male was older (marginally non-significant effect of the quadratic term; Figure 2 and Table 2). In addition, a female tended to win more intersexual conflicts when the rank difference of the heterosexual dyad in the intersexual hierarchy was small (marginally non-significant effect; Table 2). Female age and reproductive state did not influence the results.

4. Discussion

In this study, we find that adult female mandrills can occasionally elicit male submissive behaviors, and can outrank males, despite being much smaller and traditionally considered strictly dominated by males. We further find that the intersexual hierarchy represents an interdigitation of the female and male intrasexual hierarchies, is not sensitive to the behavioral dataset used for its construction, and fluctuates with sociodemographic variables such as breeding seasonality and group-sex-ratio. Below, we first discuss the biological relevance of our hierarchical inferences, before envisaging potential factors affecting the dynamics of female-male dominance relationships.

We used various methods, including David's score (David, 1987) and I&SI (de Vries, 1998), and different datasets to establish intersexual hierarchies. The average percentage of males outranked by an average female revolved around 9–16% independently of the dataset or method used to infer hierarchies. However, such a result is at odds with the percentage of agonistic interactions where females elicited male submissive behaviors, which is closer to 2% overall. Such discrepancy may reflect methodological problems or biological processes potentially specific to our study system, or a combination both; although similar discrepancies have also been reported in strictly female-dominant species, like Verreaux sifakas where females win the minority of intersexual agonistic interactions suggesting that females can indeed outrank males though they lose most fights against them (Lewis et al., 2022). Regarding methodological problems, mandrills live in exceptionally large groups and in dense forests with low visibility, making it difficult to observe interactions between all group members. Additionally, intersexual aggression is characterized by relatively low severity (Smit et al., 2022) and thus it might be easily overlooked outside focal observations. As a result, a majority (62%) of the intersexual dyads in our study group were never observed interacting agonistically (Supplementary Table S1), and such proportion is highest (92%) in those dyads where the female was found to outrank the male. This may have generated instability in the inferred hierarchies, and questions our finding that females can actually outrank some males. Specifically, establishing the hierarchy between two individuals A and B from a large group relies on direct interactions between A and B, but also on indirect interactions opposing A and B to other groupmates. When there are many missing cells in interaction matrices, indirect interactions may weigh more than direct ones in hierarchical inferences, which may generate a situation where the rank order between two individuals does not reflect the outcome of the few interactions recorded between them.

Some biological aspects of our study system may accentuate these methodological challenges. First, the seasonal changes affecting the demography of the group, with many males entering the group at the onset of the mating season and leaving afterwards (Abernethy et al., 2002; Brockmeyer et al., 2015),

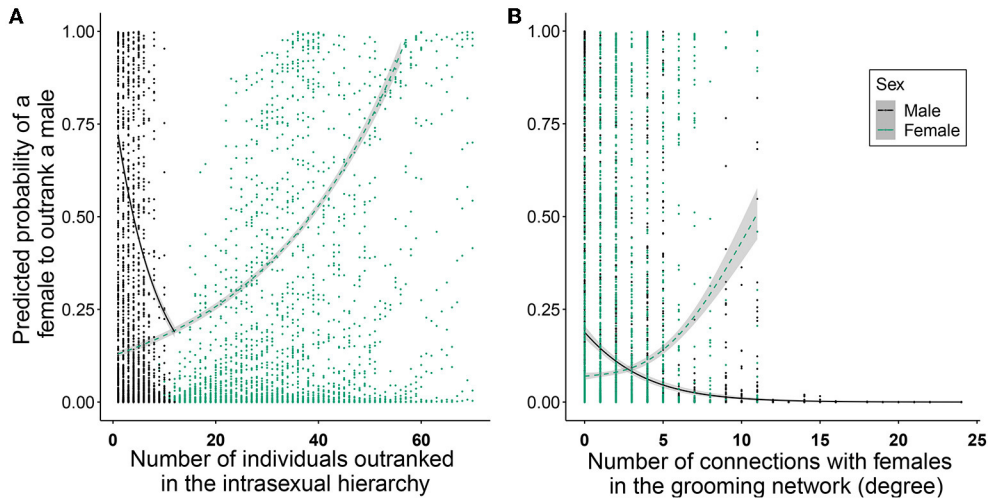

FIGURE 1
Factors influencing the probability for a female to outrank a male as a function of the **(A)** female (green-dashed line) and male (black) intrasexual rank (number of individuals outranked) and **(B)** female (green-dashed line) and male (black) number of connections (degree for males and in-degree for females) in the grooming networks. The fitted values of the GLMM are shown on the y-axis and shaded areas show 95% confidence intervals.

TABLE 1 Factors affecting the probability for a female to outrank a male (Number of observations: 5,433 dyad.seasons).

Response variable: Probability to outrank a male (0/1)

Fixed factor	Estimate	CI 95%	Chisq	*P*-value
Female rank	0.280	**[0.246;0.313]**	260.307	**<0.001**
Male rank	-0.531	**[−0.654;-0.408]**	71.602	**<0.001**
Female degree	−5.230	[−18.656;8.196]	9.081	0.445
Female degree^2	17.676	**[6.175;29.176]**		**0.003**
Male degree	-0.634	**[-0.738;-0.529]**	140.573	**<0.001**
Season (Ref: Birth)	0.934	**[0.547;1.321]**	22.423	**<0.001**
Female Age	−0.037	[−0.096;0.021]	1.559	0.212
Male Age	52.780	**[13.141;92.419]**	22.007	**0.009**
Male Age^2	41.380	**[19.025;63.735]**		**<0.001**

Random factors: 8 years; 92 females; 34 males; 1,890 dyads. Significant *p*-values and confidence intervals that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq), while the significance of each level of a categorical variable was evaluated against a reference level (noted "Ref") according to whether their confidence intervals (CI) overlap or not.

necessarily generates high instability in the male as well as the intersexual hierarchy. It is likely that there are frequent rank reversals, at least in the first half of the season, and some immigrants may remain peripheral in the days following their arrival, time to assess the social landscape. They may minimize interactions, during this period, with both male and female groupmates, which may be the typical—but transient—period where they occasionally show submission toward females. While alternative methods, like Elo-rating (Neumann et al., 2011), for calculating dominance hierarchies would, in theory, be better suited to establish hierarchies in such a system, they require highly resolved interaction matrices which are far too challenging to obtain in such large groups. Finally, the frequent use of sexual coercion by high-ranking male mandrills (Smit et al., 2022) may also result in asymmetrical patterns of interactions between male-dominant and female-dominant dyads, and explain why there are lower rates of interactions—and more missing data—in female-dominant than male-dominant dyads. While males may often direct aggression to subordinate females in male-dominant dyads in a context of sexual coercion (Smit et al., 2022), females may not bother about harassing those males they outrank. Indeed, male-dominant dyads interact agonistically over twice as often as female-dominant ones (3.3 ± 4.8 vs. 1.6 ± 1.1 times; ±SD).

Altogether, these results highlight the caution needed when interpreting the biological relevance of hierarchies emerging from datasets with high number of non-interacting dyads and in our case, female mandrills may occasionally outrank males but potentially in a lower frequency than our results indicate.

Nevertheless, our results show that females can occasionally elicit male submissive behaviors and suggest that strict male dominance is unlikely in this species. Despite the apparently low predictive power of hierarchical inferences at the dyadic level, the temporal fluctuations of the average percentage of males outranked by females may still reflect genuine changes in the temporal dynamics of intersexual dominance. In line with this, we find that females outrank more males during the mating than during the birth season. Such seasonal changes may be related to variation in individual reproductive states and associated needs (Murie and Harris, 1988; Jawor, 2000), motivation or leverage (Lewis, 2002, 2018; Davidian et al., 2022). In particular, when females have some reproductive control (i.e., control over when and with whom to mate), as in most lemurs (Hohenbrink et al., 2016; Lewis et al., 2022), they typically have more leverage when sexually receptive because males who try to mate with them may avoid to aggress them (Lewis, 2002; Davidian et al., 2022). Yet, additional results show that sexually receptive female mandrills are not more likely to win conflicts against males compared to females in other reproductive states, possibly because they have low reproductive control due to frequent sexual coercion (Smit et al., 2022). Instead, this result may reflect demographic changes due to the influx of male mandrills in the social group at the beginning of that season. An increased number of males may lead to frequent male-male fights, with some males falling below some females at the bottom of the hierarchy, a so-called "winner-loser" effect which is known to affect intersexual dominance in other species (Hemelrijk et al., 2008, 2020).

Alternatively, temporal changes in intersexual dominance may reflect deeper changes in the social dynamics of mandrill groups across seasons. During the mating season, when males are more numerous, they may adopt alternative reproductive tactics. High-ranking resident male mandrills may compete to mate-guard ovulatory females, while low-ranking immigrants may remain transient and peripheral and try to get sneaky matings (similarly to rock hyraxes Bar Ziv et al., 2016) without

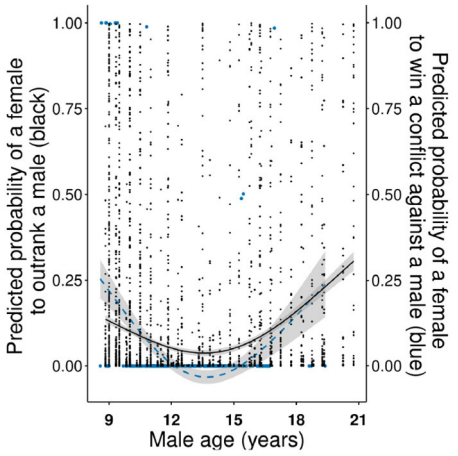

FIGURE 2
Male age in relation to the probability for a female to outrank a male (black) and win a conflict against a male (blue-dashed line). The fitted values of the GLMMs are shown on the y-axes and shaded areas show 95% confidence intervals. For graphical purposes the quadratic term of male age is shown, although its effect on the probability to win an intersexual conflict was marginally non-significant ($p = 0.093$).

TABLE 2 Factors affecting the probability for a female to win a conflict against a male (Number of intersexual conflicts: 382).

Response variable: Probability to win an intersexual conflict (0/1)					
Fixed factor	**Level**	**Estimate**	**CI 95%**	**Chisq**	***P*-value**
Rank difference		−23.333	[−49.563;2.897]	3.040	0.081
Reproductive state	Swollen (Ref: Non-Swollen)	17.167	[−17.347;51.682]	1.281	0.734
	Pregnant (Ref: Non-Swollen)	6.661	[−14.758;28.080]		
	Lactating (Ref: Non-Swollen)	9.501	[−18.957;37.959]		
	Pregnant (Ref: Swollen)	−6.086	[−27.915;15.743]		
	Lactating (Ref: Swollen)	−2.370	[−29.530;24.790]		
	Lactating (Ref: Pregnant)	5.914	[−51.749;63.577]		
Male Age		−173.450	**[−309.137;-37.763]**	7.324	**0.012**
Male Age^2		103.888	[−17.220;224.996]	7.324	0.093
Female Age		0.342	[−1.274;1.958]	0.172	0.678

Random factors: 8 years; 41 females; 20 males; 182 dyads. Significant *p*-values and confidence intervals that did not cross zero appear in bold. The significance of each variable was assessed using chi-square tests (Chisq), while the significance of each level of a categorical variable was evaluated against a reference level (noted "Ref") according to whether their confidence intervals (CI) overlap or not.

establishing clear dominance relationships with females. Our result that less socially integrated males are less dominant over females, and that females preferentially outrank young and old males support this interpretation. Overall, those males who take an active part to the social dynamics of the group may simultaneously rise in rank, while females may only outrank those males who may lack the confidence or motivation to confront females or rivals, as may occur in other mammals (Van Schaik and Paul, 1996; Mysterud et al., 2003; Silk et al., 2020). Finally, female mandrills outrank more males when they are more socially integrated in the female social networks, which may reflect males' reluctance to confront well-connected females who may support each other against males (Setchell et al., 2006a). Such coalitions have also been observed in other primates living in polygynandrous groups where females are philopatric (geladas: Dunbar, 1975; Guinea baboons (*Papio papio*): Goffe et al., 2016) and may often contribute to counter-balance male-biased dominance in species where physical asymmetries between sexes are extensive.

This study contributes to a growing body of evidence that draws a more dynamic landscape of female-male dominance relationships, where intersexual dominance can fluctuate across time and contexts. Our results suggest that females may outrank a small proportion of males in a highly dimorphic nonhuman primate, although this remains to be confirmed due to limits in the resolution of our datasets. We further found that females outrank more males during the mating season and when they are high-ranking and more socially integrated; while they preferentially outrank poorly socially integrated males with low competitive abilities. These results point to the importance of social integration and seasonal breeding, and of associated demographic and motivational shifts in males and females, to explain the dynamics of intersexual dominance, and contribute to a new area aimed at understanding the dynamics of female-male power struggles at an individual scale.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: GitLab https://gitlab.com/nksmt/mandrills2.

Ethics statement

The animal study was reviewed and approved by CENAREST Institute (permit number, AR0060/18/MESRS/CENAREST/CG/CST/CSAR).

Author contributions

NS, EH, and MC designed the study and contributed to writing the manuscript. NS performed the statistical analyses and wrote the first version of the manuscript. MC, NS, and BN contributed to data collection and database management. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

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ORIGINAL RESEARCH
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Intersexual Agonism in Gray Langurs Reflects Male Dominance and Feeding Competition

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Male-female agonism varies throughout the primate order with males often dominating females, especially in sexually dimorphic species. While intersexual agonism has been attributed to sexually coercive contexts, it can also occur for other reasons and intersexual dominance may be influenced by the adult sex ratio. If the proportion of males is high, certain males will regularly lose against other males. Loser-effects may then pave the way for some females to dominate these males, an effect that has been described in a few primate species. Here we investigated the frequency, general style, and context of agonism among gray langurs (*Semnopithecus* spp.). Data were collected at two study sites, at Jodhpur, India (one group), and at Ramnagar, Nepal (two groups). The adult sex ratio varied between 0.077 and 1.000 males to females. At both sites, data on agonistic interactions (aggression and submission) were collected in continuous focal animal and *ad libitum* sampling techniques during 1,945 contact hours (including 1,220 focal animal hours, total). Although aggression intensity was low, high directional consistency and the rare occurrence of counteraggression suggested a despotic dominance style, a likely prerequisite for dominance effects based on adult sex ratio. Aggression by females against males was very rare and mainly occurred in the defense of offspring. We found little evidence for partial female dominance regardless of adult sex ratio. In a few cases in which a female had a higher dominance index than a male, she did not dominate this male in dyadic encounters. Agonism by males directed at females occurred mainly in a feeding context while male policing and a sexual context were both rare. The latter was mostly restricted to females after they had harassed a sexual interaction or after they had behaved proceptively toward a male. Our study suggests that across species the effect of adult sex ratio on female dominance might be more variable than previously suggested. The fact that most agonism between males and females occurred over food identifies intersexual feeding competition as a new research avenue with potentially important consequences for existing ideas on the costs and benefits of group life and composition.

Keywords: adult sex ratio, aggression, counteraggression, despotism, dominance index, offspring defense, sexual coercion, submission

INTRODUCTION

Agonism among the members of group-living animals is often viewed as a sex-specific behavioral strategy. Male mammals are commonly seen as competing with other males for access to females (Darwin, 1871), and females are usually assumed to compete over access to food or safety or both (Wrangham, 1980; van Schaik, 1989). While the reality is much more complex (Clutton-Brock, 2021), these ideas form the basis of so-called socio-ecological models that relate to the number of males in a group and relationships among males (Emlen and Oring, 1977; Carnes et al., 2011; Koenig et al., 2013; Ostner and Schuelke, 2014) as well as to the links between ecology and female social relationships (Wrangham, 1980; van Schaik, 1989; Isbell, 1991; Sterck et al., 1997; Koenig, 2002; Koenig et al., 2013). Over the years, however, it has become clear that these models do not reflect the existing variation in individual behavioral strategies and emerging social systems (van Schaik, 1996; Clutton-Brock and Janson, 2012). Importantly, when focusing on same-sex interactions, the interactions between members of both sexes and their possible influence on the social structure are not being addressed (Kappeler, 2017). As more results have accumulated, it has become particularly evident that male dominance over females and male aggression against females varies tremendously across non-human primates (Hemelrijk et al., 2008; Muller et al., 2009), but its potential impact on social structure and competition in general has remained largely unexplored. While intersexual relationships are certainly also affected by benefits that males and females can provide to each other when residing in a group together, e.g., through predator detection, during intergroup encounters, or as coalitionary support (e.g., Rose, 1994; Perry, 1997; Ostner et al., 2013; Archie et al., 2014), in the following we will focus on intersexual agonism and dominance.

Intersexual Agonism and Partial Female Dominance

Based on general fighting ability and in the absence of female-female coalitions, it is typically assumed that in sexually dimorphic primate species, males dominate females (Smuts, 1987). While this may be true for a number of primate species, more and more studies have emerged in which females have been shown to exhibit frequent aggression against males or to even dominate some or several males in their group (Smuts, 1987; Hemelrijk et al., 2020; Izar et al., 2021). Generally, such partial female dominance has thus far only been documented for despotic species (despotic *sensu* de Waal and Luttrell, 1989; Preuschoft and van Schaik, 2000; Thierry, 2000; Flack and de Waal, 2004) and among other factors it seems to be related to the adult sex ratio of a study group (Hemelrijk et al., 2008; Kappeler, 2017). Females are suggested to dominate more males or a larger proportion of the males present in a group possibly because (i) more males can mean more contest competition among males, increasing winner-loser effects among males, allowing females to take advantage and dominate males who frequently lost and/or because of (ii) generally higher and more intense female aggression toward males in groups with more males (Hemelrijk et al., 2008, 2020; Stroebe et al., 2017; Izar et al., 2021). However, larger groups with more males can also mean increased agonism of males toward females (Kappeler, 2017), which begs the question if partial female dominance is possible under increased male aggression. Clearly, more studies on intersexual dominance are needed to examine if the proposed effects of adult sex ratio on partial female dominance in despotic species hold.

Functions of Male Aggression and Partial Female Dominance

Apart from the questions of how and when intersexual dominance varies among non-human primates, it is equally important to determine what primate males may achieve through agonism toward females or conversely, what costs females are facing at the receiving end and what they could thus gain through intersexual dominance (Smuts, 1987; Smuts and Smuts, 1993; Muller et al., 2009). Starting with Smuts (1987) and Smuts and Smuts (1993) groundbreaking studies, the focus primarily has been on sexual coercion particularly sexual harassment and forced copulations (for a discussion of direct and indirect forms of sexual coercion see Muller et al., 2009). In recent years, this focus has been reinforced through detailed, long-term data for chacma baboons, hamadryas baboons, and chimpanzees (Muller et al., 2007, 2009, 2011; Swedell et al., 2014; Baniel et al., 2017; Watts, 2022). From a female perspective, partial female dominance may reduce sexual coercion and increase the extent of female mate choice (Smuts and Smuts, 1993; Hemelrijk et al., 2020). However, while sexual coercion can be common and can have important implications for female and male fitness, it is not the norm among primates (van Schaik et al., 2004). It is especially rare in lemuroids and platyrrhines and occurs in about 50% of catarrhines studied thus far, particularly in species that are prone to infanticide by males (van Schaik et al., 2004; following Muller et al., 2009, we consider infanticide as a third form of sexual coercion in which aggression is not directed at a female herself but her infant). To what extent this variation relates to partial female dominance is unclear at present, making studies of intersexual dominance in species with infanticide an important test case.

Nonetheless, male aggression against females is not solely related to sexual coercion. It has also been suggested to occur in four other general contexts: feeding competition, male policing (i.e., male intervention in female-female conflicts), status competition, and redirected aggression (Muller et al., 2009). While male agonism against females has been well documented in species with strong intergroup feeding competition, such as capuchins and chimpanzees (Muller et al., 2009; Scarry, 2013), only few detailed studies have addressed intersexual within-group feeding competition in primates. In fact, even fewer studies have reported the context of intersexual agonism (e.g., wedge-capped capuchins; O'Brien, 1991; see also Smuts and Smuts, 1993). In general, it can be expected that intersexual feeding competition may be more prominent in species relying on monopolizable food resources (Muller et al., 2009). Similarly, male policing occurs for example in mountain gorillas and Thomas langurs (overview in Watts et al., 2000), but it is unclear if male policing can explain most of the intersexual agonistic interactions in

these or other species. Lastly, there is little evidence for status competition and redirected aggression as a major source of intersexual agonism (Muller et al., 2009). Given the major impact that sexual coercion can have on a female's fitness, intersexual feeding competition may be the only other source of conflict that could have a strong impact. Judging by the effect of scramble and contest competition on female birth rates (Pusey, 2012), males contesting with females over access to food would heighten the already existing feeding competition among females. Consequently, intersexual agonism by females and partial female dominance over males would reduce both sexual coercion and competition over food for females. However, few studies have taken on such a functional perspective.

Study Species and Aims of the Study

Here we studied intersexual agonism and dominance among gray langurs (*Semnopithecus* spp.; taxonomy following Arekar et al., 2021). Gray langurs are suitable subjects for the topic of intersexual agonism for several reasons. First, the study populations in Jodhpur, India (*S. entellus*) and in Ramnagar, Nepal (*S. schistaceus*) are characterized by despotic male-male and despotic female-female relationships because agonism is overall frequent and relationships are unidirectional and transitive (Borries et al., 1991; Borries, 1993; Koenig, 2000; Lu et al., 2008; Perlman et al., 2016; Sommer, pers. com.). This may make it likely that male-female relationships are despotic as well. If true, the entire social system would be despotic, a prerequisite for partial female dominance as described by Hemelrijk et al. (2008). Second, while female and male dominance hierarchies can be unstable, dominance has a significant impact on reproductive success of males and females in both populations (Sommer and Rajpurohit, 1989; Borries et al., 1991; Launhardt et al., 2001; de Vries et al., 2016). Thus, in addition to despotic social relationships (despotic *sensu* de Waal and Luttrell, 1989), reproductive skew is high (despotic *sensu* Vehrencamp, 1983). Third, females of both populations have been shown to compete primarily over monopolizable food resources (Borries, 1993; Koenig et al., 1998) with most agonism occurring over food (Koenig and Borries, 2006). Fourth, males vigorously fight over access to females (Sommer, 1988; Borries, 2000) and males in both populations regularly commit infanticide with more than 30% of infant mortality attributed to it (Borries and Koenig, 2000). Lastly, at Ramnagar a substantial amount of male-male agonism also occurred over food (a quarter to one-third of the conflicts; Koenig and Borries, unpublished).

Given the general characteristics of the study species and the predictions about intersexual agonism and dominance, in the current study we first tested if male-female agonistic relationships were despotic, a prerequisite for partial female dominance. If this would be the case then aggression would be rare, but of high intensity, directional consistency would be high, and counteraggression rare (de Waal and Luttrell, 1989; Preuschoft and van Schaik, 2000; Thierry, 2000; Flack and de Waal, 2004). Next, we examined how often and in what contexts females behaved aggressively toward males. Following Hemelrijk et al. (2008), we then analyzed dominance indices, expecting an effect of adult sex ratio on partial female dominance over males, i.e., females being more often dominant with increasing proportion of males in the group. Lastly, we analyzed the possible functions of male agonism toward females by determining how frequently the context of agonism was related to sexual coercion, feeding competition, or male policing (cf. Muller et al., 2009). We excluded two suggested contexts: (i) status competition because in gray langurs males leave their natal group as immatures and only adult males immigrate (Rajpurohit and Sommer, 1993; Borries, 2000), and (ii) redirected aggression by a male because it did not occur.

MATERIALS AND METHODS

Study Locations and Groups

Data were collected on one group of wild, provisioned gray langurs (*Semnopithecus entellus*) near Jodhpur, India around lake Kailana (240 m a.s.l., 26°17'N, 72°58'E; Winkler, 1981) as well as two neighboring groups of wild, unprovisioned gray langurs (*Semnopithecus schistaceus*) living in a semi-evergreen forest near Ramnagar, Nepal (300 m a.s.l., 27°44'N, 84°27'E; Podzuweit, 1994). Both sites are rather seasonal in weather and food availability (Winkler, 1981; Koenig et al., 1997), although at Jodhpur the effect of seasonality is weakened because of provisioning and reproduction is seasonally restricted only at Ramnagar (Sommer and Rajpurohit, 1989; Koenig et al., 1997).

All individuals in the three groups differed in their stature, coat color, scars, broken fingers, broken tails, or other traits so that they could be distinguished individually. Additionally, at Ramnagar, each female had a hairless skin area ventral to the callosities between the thighs (pubic patch; e.g., Bernstein, 1968) which was uniquely dotted with depigmented (pink) spots (Podzuweit, 1994).

At Jodhpur, the Kailana I group (or B19; hereafter KI group) was regularly provisioned by local people to the extent that provisioned food amounted to one-third of the total feeding time (Winkler, 1984). Throughout the study period, the group had one adult male (who had been in the group for 19 months prior to the beginning of data collection) and 13 adult females resulting in an adult sex ratio of 0.077. No females matured during the study period and group size ranged from 18 to 23 individuals, because of births and infant deaths.

The two groups studied at Ramnagar, A group and O group, varied in size and composition during the study period, but A group was consistently the "small" group, at around 10 individuals in total (range 9–10), and O group the "big," at approximately 30 individuals (range 26–34; population mean 18.3 individuals; Koenig, 2000). The A group consisted of 1, 2, or 3 adult males and 2 or 3 adult females (4–6 adult individuals in total). The number of adults varied because of emigration (2 adult males) and death (1 adult female) as well as immigration (1 adult female; the only immigration of an adult female ever observed in this population; Koenig et al., 1998) resulting in variable adult sex ratios [1.000 (3:3, 2:2), 0.667 (2:3), and 0.333 (1:3)]. O group consisted of 3 or 5 adult males and 15 adult females (18 or 20 adult individuals). The number of adults varied because two adult males immigrated and assumed the alpha

and beta positions. The other three males remained as lower ranking males. Subsequently, three infants likely fell victim to infanticide (Borries, 1997) and one of the respective mothers also disappeared. At the same time, one subadult female entered the adult female hierarchy and was considered an adult. This resulted in two different adult sex ratios of 0.200 (3:15) and 0.333 (5:15) for O group.

Data Collection

At both sites, data were collected *via ad libitum* and focal animal sampling techniques (Martin and Bateson, 2007). Focal animal samples lasted for 30 min and combined continuous and instantaneous recording (at 30 s intervals). Within an observation period, focal individuals were sampled evenly across all hours of the day from dawn to dusk. As data collection involved the study of focal animals, data were not recorded blindly; however, the sequence of focal animals was randomized for each observation period.

At Jodhpur, CB collected behavioral data on adult females of KI group from January 07 to October 26, 1985 (inclusively) during three distinct periods lasting 45, 97, and 56 days, respectively (see Table I in Borries et al., 1991, p. 236). During the first two periods, eight females were focal animals, and during the last period, six females. The total contact time with KI group was 1,018.5 h of which 569.0 h were spent in focal animal sampling.

At Ramnagar, AK collected behavioral data on all adult individuals (males and females) in A group and O group from January 9, 1994 to January 23, 1995 (inclusively). In A group, data were collected over seven periods (mean 7.9 days/period) and in O group over four periods (mean: 26.3 days/period). Periods were distributed over the course of a year to capture seasonal changes in food availability as well as the mating and the birth season. The total contact time with A group was 257.0 h, of which 152.0 h were spent in focal animal sampling. In group O it was 669.3 h of contact time with 499.0 h of focal animal sampling.

Agonistic behavior was recorded during focal animal continuous sampling as well as *via ad libitum* sampling during the entire contact time with a group. We defined agonism as all aggression and submission. Following Rowell (1974), we included displacement within submissive behavior, i.e., being displaced: an individual A is giving up its place, food, social partner, etc. in favor of an approaching individual B or following aggression by individual B. Agonistic behaviors included in this study were recorded as behavioral acts, which have been described and defined elsewhere (Dolhinow, 1978; Sommer, 1985; Borries, 1989; see also **Supplementary Table 1**) and the same ethogram was used at both study locations. Behaviors considered here have previously been shown to occur in an agonistic context (Borries, 1989; Lu et al., 2008). Because this was not always clear for vocalizations, we did not include vocalizations in the analyses.

While recording agonistic behavior, the context was noted as well. The following contexts were distinguished: (i) food, i.e., agonism occurred while one or both individuals were feeding or one of the interactants was replaced at a feeding site or both; (ii) place, i.e., if agonism occurred at a specific location (e.g., regularly used to monitor or to rest) which was initially occupied by one individual and at the end of the interaction it was occupied by the other individual; (iii) after a sexual harassment, i.e., a sexual interaction was interrupted by a third individual usually *via* approaching and vocalizing, whereupon the male (not the female) of the pair showed agonism toward the harasser; (iv) sexual behavior, i.e., following sexual behavior (which could be mating or solicitation etc.), the male showed agonism toward the female and thus terminated the sexual interaction; (v) policing, i.e., aggressive behavior was directed at one of two individuals already engaged in an agonistic interaction; (vi) social, i.e., preceding an agonistic interaction, one individual was engaged in allogrooming or was in body contact or was close to a (any) group member; (vii) infant; i.e., a female fled, carrying her infant after having been approached by a male who reached for her infant; (viii) unknown; all remaining cases. These context definitions were applied very conservatively in the Jodhpur study, resulting in an overall lower percentage of identified contexts in comparison to the Ramnagar study.

Data Analysis

In the analysis, we considered individual behavioral acts as well as bouts. A bout was defined as a temporal cluster of agonistic acts in an interaction between two (or more) individuals (see also Martin and Bateson, 2007). Bouts were considered decided if one individual won because the other individual gave up its place or item or signaled submission (Hausfater, 1975). Bouts were undecided if the interaction ended in a draw, e.g., no individual gave up its place or item after one or more agonistic acts (for coalitions see below). Because of a small sample size for females with infants, we did not distinguish whether a female had an infant clinging to her belly or not during an agonistic bout. For the analysis of rates of behavior, we used data exclusively from focal animal sampling, calculating the number of occurrences per focal observation hour. For all other analyses, we combined data from focal animal and *ad libitum* sampling.

In the results below, we first generally describe intersexual agonism regardless of the sex of the actor by listing the occurrence and rates of different types of agonism (aggression, submission). Because groups differed in size and composition, we describe the intersexual agonism per group.

In the analysis of despotism, we considered three criteria: intensity of aggression, directional consistency of all agonistic acts, and counteraggression (de Waal and Luttrell, 1989; Preuschoft and van Schaik, 2000; Thierry, 2000; Flack and de Waal, 2004). We categorized intensity of aggression following Lu et al. (2008; see Table 3 in Lu et al., 2008; see also **Supplementary Table 1**). To ease comparison with other studies, we also provided a breakdown of contact and non-contact aggression (**Supplementary Table 1**). Using the program MatMan (de Vries et al., 1993), we evaluated directional consistency by calculating the directional consistency index (DCI; van Hooff and Wensing, 1987) for all behavioral acts noted for intersexual agonistic interactions. If a single adult acted against more than one adult simultaneously, all recipients received a score. Counteraggression by females was defined as any aggressive act by a female in response to an aggression received by a male.

To investigate partial female dominance, we first examined how often and in which context females showed spontaneous aggression toward males. This was done to understand if aggression (and winning) by females is confined to certain contexts or is context independent, also referred to as "spheres of dominance" (Hand, 1986; Preuschoft and van Schaik, 2000). Furthermore, to study the proposed relationship between partial female dominance and adult sex ratio, we calculated dominance indices following Hemelrijk et al. (2005, 2008). Using only decided agonistic bouts, we first calculated the proportion of winning for each member of a dyad. If individuals were never observed to interact, the respective dyad was excluded from the analysis. To rank individuals, we used the average dominance index (ADI) for each individual, which was calculated as the average of all its dyadic dominance indices (Hemelrijk et al., 2005). Based on this ranking, we calculated the female dominance index (FDI; Hemelrijk et al., 2008). Here, each male with an ADI lower than a female was counted as one (dyad), and all dyads in which a male ranked below a female were summed up. In the case of a tie between a male and a female, 0.5 was added. The sum for all male-female dyads was then divided by the number of males each female theoretically could dominate summed over all females (i.e., the number of males multiplied by the number of females) to determine the female dominance index. This FDI runs from 0.0 (complete male dominance) to 1.0 (complete female dominance).

To investigate the context of male agonism against females, we considered bouts instead of individual acts, which prevents context inflation because a bout may involve several agonistic acts.

RESULTS

Male-Female Agonistic Relationships

Male-Female Dominance Style

Intersexual agonism, i.e., agonism between males and females regardless of the actor, occurred at a rate of 0.074, 0.174, and 0.112 acts per focal hour for KI group, O group, and A group, respectively. It was primarily characterized by submission (50.3–88.2%; **Table 1**), which by itself was dominated by displacements (see **Supplementary Table 1** for details). This was also reflected in the rates of agonistic acts. With 0.030, 0.044, and 0.013 acts per focal hour (for KI group, O group, and A group, respectively), rates of aggression were less frequent in all three groups compared to submission which occurred at 0.044, 0.130, and 0.100 acts per focal hour.

Of all aggressive behaviors, low intensity ones were more frequent than high intensity ones (59.1–100.0%, **Table 1**). Unsurprisingly, the percentage of aggression, particularly of high intensity aggression, dropped when only focal animal samples were considered, and consequently the percentage for low intensity aggression and submission increased. This indicates that interactions of high intensity were discovered and thus recorded more frequently during *ad libitum* sampling (see also Martin and Bateson, 2007). This effect was larger at Ramnagar than at Jodhpur, likely, because of the poorer visibility at Ramnagar, which can bias toward the detection of high intensity behavior such as chases rather than the more subtle submission.

Aggression and submission varied widely across groups (**Table 1**). Aggression, and specifically high intensity aggression, was most frequent in the single male group KI (35.3–40.9%) but

TABLE 1 | Intersexual agonistic behavior and intensity of aggression in gray langurs independent of the sex of the actor.

Group	Methods	Type	Percentage (*n*)	Sub-type	Percentage (*n*)
KI	*Ad libitum* and focal	Aggression	49.7 (88)	High intensity	40.9 (36)
				Low intensity	59.1 (52)
		Submission	50.3 (89)		
	Focal	Aggression	40.5 (17)	High intensity	35.3 (6)
				Low intensity	64.7 (11)
		Submission	59.5 (25)		
O	*Ad libitum* and focal	Aggression	39.5 (92)	High intensity	39.1 (36)
				Low intensity	60.9 (56)
		Submission	60.5 (141)		
	Focal	Aggression	25.3 (22)	High intensity	22.7 (5)
				Low intensity	77.3 (17)
		Submission	74.7 (65)		
A	*Ad libitum* and focal	Aggression	23.1 (6)	High intensity	
				Low intensity	100 (6)
		Submission	76.9 (20)		
	Focal	Aggression	11.8 (2)	High intensity	
				Low intensity	100 (2)
		Submission	88.2 (15)		

For each group and method, aggression and submission sum up to 100%. Categorization by intensity follows Lu et al. (2008). For each group and method, the aggression sub-types (high and low intensity) sum up to 100%. The number of acts are given in parenthesis. See ***Supplementary Table 1*** *for a detailed breakdown of behavioral acts included in types and sub-types as well as a categorization into contact and non-contact aggression; ad libitum and focal: ad libitum and focal animal sampling technique; focal: focal animal sampling technique.*

was lower than the percentage of low intensity aggression. In O group with 3 and 5 males, aggression accounted for 25.3–39.5% of the agonistic acts, but the percentage of high intensity aggression out of all aggression was low (under 40%). In the smallest A group with the most even adult sex ratio, aggression was rare, and none was of high intensity.

Agonistic interactions between males and females had a high directional consistency with DC indices between 1.000 and 0.796 (**Table 2**). The larger groups with a more skewed adult sex ratio and many more interactions (KI and O) had lower directional consistencies (0.796–0.948) than the small A group (DCI 1.000) with a more even sex ratio and much fewer interactions.

Female counteraggression against males was overall very rare. During *ad libitum* and focal animal sampling, a female never responded to male agonism with aggression in groups KI and A. In O group, female counteraggression occurred three times and only during *ad libitum* sampling. In two cases, the female slapped a male after being chased/jumped on by him. The context of these two cases could not be determined. In a third case, the female initially harassed a male-female consortship, which resulted in the respective male chasing her. She responded by slapping the male.

Do Females Dominate Males and Under Which Circumstances?

In this section, we first describe the occurrence and context of spontaneous aggressive acts of females against males to see if aggression is context dependent or independent. Noteworthy, an aggressive act does not necessarily equal winning an agonistic bout. The winner of a bout will occupy the space or item that the loser gave up or the winner will receive submission. These decided interactions are used in the subsequent analysis of dominance indices and the relationship between partial female dominance and adult sex ratio.

Although rare, spontaneous aggression by females toward males occurred in KI and O groups (details below). It was not observed in A group. Male submission toward a female was even less frequent (in KI and O group), and again not observed in A group.

In KI group we observed 13 bouts in which females behaved aggressively toward the male, 12 of these encounters had a single female aggressor. These 12 bouts also included 5 submissive behaviors by the male. They occurred at a rate of 0.007 per hour or once every 142 focal hours. In O group we observed 23 bouts in which females were the aggressor, 19 of these encounters included a single female. These 19 bouts also included 2 submissive behaviors by males. Bouts with female aggressors (or male submission) occurred at a rate of 0.004 per hour or once every 250 focal hours.

Spontaneous aggression by a single female against the male in KI group did not occur in a particular context (**Table 3**). For most bouts (66.7%), no specific context could be determined. It did occur twice in a social context, once over food, and once as aggression redirected at the male after a female-female conflict. In O group, aggression by a single female against a male occurred most often when a female harassed a sexual interaction of the male with another female (37.5%). Importantly, all these sexual harassments were performed by the same individual female, but her targets were different males and females. Females were also aggressive when males came close to or approached young infants (25.0%) and one female defended her older, weaned male offspring against aggression by adult males (12.5%). Unknown (12.5%), food (6.4%), and after sexual behavior were the other remaining contexts. It is noteworthy, that aggression by coalitions of females against males (not included in **Table 3**) mainly occurred when a male approached or came close to a young infant (KI group: 1 of 1; O group: 3 of 4, 1 = unknown context).

To determine the extent to which females dominated males, we compared dominance indices (**Table 4**; see also **Supplementary Tables 2–7** for details). In KI group, females never outranked the male and the FDI was 0.0. In other words, the ADI of the male was higher than the ADIs of every female in the group. In addition, while females occasionally won against the male, never did a female win more often than the male did (**Supplementary Table 2**). In O group when it had 3 adult males, all males had higher ADIs than all females and the FDI was 0.0. Again, winning by a female occurred, but in all dyads males won more often than females (**Supplementary Table 3**). In O group when it had 5 adult males, one of the females had a higher ADI than two of the males resulting in an FDI of 0.03. However, this

TABLE 2 | Directional consistency index (DCI; van Hooff and Wensing, 1987) for intersexual agonistic acts among gray langurs.

Group	*n* Males	*n* Females	*n* Agonistic acts	DCI
KI	1	13	170	0.800
O	3	15	116	0.948
O	5	15	108	0.796
A	1	3	10	1.000
A	2	3	9	1.000
A	2	2	0	
A	3	3	7	1.000

Because group composition varied through immigration, death, and disappearances, DCI was calculated for each different group composition.

TABLE 3 | Spontaneous aggression by a single female against a male in gray langurs.

	KI group		O group	
Context	***n* Bouts**	**Percentage**	***n* Bouts**	**Percentage**
Food	1	8.3	1	6.3
After sexual behavior			1	6.3
Sexual harassment			6	37.5
Social	2	16.7		
Redirected	1	8.3		
Male approaches infant			4	25.0
Support weaned offspring			2	12.5
Unknown	8	66.7	2	12.5
Total	12	100.0	16	100.0

Observations based on ad libitum and focal animal sampling techniques. Excluding 3 bouts with female counteraggression in O group. For context descriptions and female coalitionary aggression see text. Spontaneous aggression by females against males was not observed in A group.

TABLE 4 | Group composition, adult sex ratio, and dominance indices for gray langurs based on decided agonistic bouts of all adult individuals.

Group	*n* Males	*n* Females	ASR	Male proportion	*n* Decided bouts	FDI	Ranking from high to low based on ADI
KI	1	13	0.077	0.071	1,474	0.00	M,F,F,F,F,F,F,F,F,F,F,F,F
O	3	15	0.200	0.167	373	0.00	M,M,M,F,F,F,F,F,F,F,F,F*,F*,F,F,F,F,F
O	5	15	0.333	0.250	480	0.03	M,M,M,F,M,M,F,F,F,F,F*,F*,F,F,F,F,F,F,F,F,F
A	1	3	0.333	0.250	65	0.00	M,F,F,F
A	2	3	0.667	0.400	12	0.08	M,M*,F*,F,F
A	2	2	1.000	0.500	3		not calculated; too small sample size
A[a]	3	3	1.000	0.500	16	0.17	M,M*,F*,F*,F

ASR, adult sex ratio (n males/n females); male proportion, proportion of males on all adults; FDI, female dominance index (Hemelrijk et al., 2008); ADI, average dominance index (Hemelrijk et al., 2005). Adult sex ratios and male proportions varied because of immigration, death, and disappearances.
[a]*One male did not interact and was excluded, *individuals had the same ADI.*

female lost all encounters with the two males who had a lower ADI than she did. In addition, in this 5-male constellation, two females with ADIs lower than all males, nevertheless won against individual males (2 dyads total; **Supplementary Table 4**). Lastly, in group A the FDI ranged between 0.0 and 0.17. It was 0.0 for the constellation of one male and three females, 0.08 for 2 males and 3 females, and 0.17 for 3 males and 3 females. Noteworthy, in no case did an individual female win against a male (**Supplementary Tables 5–7**). The FDIs larger than zero are likely an artifact of small sample size and a lack of interactions resulting in several unknown relationships (**Supplementary Tables 6**, **7**).

Contexts of Male Agonism Against Females

Most of the agonism by males directed at females occurred in a feeding context (**Table 5**). This could be a simple approach-retreat interaction at a feeding location or could include aggression. Food related agonism by males occurred most often at Ramnagar (A group: 94.1%; O group: 57.3%) and was less common at Jodhpur (21.5%). But given that in the latter population most contexts (60.7%) were not determined, feeding was also the most frequently determined context. If only known contexts are considered, food makes up more than 50% of the contexts in all three groups (KI group: 54.8%, out of $n = 42$; O group: 73.5%, out of $n = 117$; A group: 100.0%, out of $n = 16$).

Male intervention in conflicts occurred but was rare (see "policing" **Table 5**). In KI group, the male always intervened on behalf of the loser. In three cases those were conflicts between adult females, and in one case he supported a juvenile male in a conflict with its mother. In O group a male intervened once on behalf of a winner in a female-female conflict. Male interventions were not observed in A group.

Agonism by males related to a sexual context was also rare, occurring in two main situations: (i) directed at a female who had harassed a sexual interaction, or (ii) after a sexual interaction with the very female. In both KI group (1.9%) and O group (4.7%) males behaved aggressively toward females who approached or actively harassed a sexual interaction between the male and another female. In the same two groups (KI group: 3.7%, O group: 1.3%), males behaved aggressively after females had directed proceptive behavior at them. Only in the remaining two cases in O group was a male aggressive during a sexual interaction. In one case this happened following a harassment by another female. In the other case, a male chased a female after a copulation attempt.

DISCUSSION

Male-Female Agonistic Relationships

Male-Female Dominance Style

We found that in gray langurs intersexual agonistic relationships were characterized primarily by female submission toward males. If aggression by males occurred, it was predominantly of low intensity. Overall, the directionality of interactions was very consistent and counteraggression by females against males was rare. Using the criteria developed for male-male as well as for female-female relationships, these results match to some extent the definition of a despotic dominance style (de Waal and Luttrell, 1989; Preuschoft and van Schaik, 2000; Thierry, 2000; Flack and de Waal, 2004). The notion of despotism is also supported by the fact that female gray langurs use bare-teeth displays in agonistic interactions. Such signals of submission are only expected in despotic species (Preuschoft and van Schaik, 2000).

Contrasting with the finding of despotic intersexual relationships is the relatively low amount of high intensity aggression, perhaps indicating a less despotic dominance style. Alternatively, it may suggest a weaker correlation between directional consistency, counteraggression, and high intensity aggression than theoretically predicted (de Waal and Luttrell, 1989; Thierry, 2000). This would fit to the idea that intersexual relationships in gray langurs are less despotic than, for example, in rhesus macaque females but more despotic than in stump-tailed macaque females, supporting the notion that the despotic-egalitarian dominance distinction is less categorical and more gradual (Preuschoft and van Schaik, 2000; Thierry, 2000).

The low amount of high intensity aggression does not, however, mean that females do not potentially suffer from aggression by males. At both study sites, the frequency of aggression by gray langur males directed toward females was clearly lower than what has been found, for example, in chimpanzees, chacma baboons, or hamadryas baboons (Muller et al., 2007, 2009, 2011; Swedell et al., 2014; Baniel et al., 2017; Watts, 2022). Nonetheless, male aggression can reduce female fitness because incoming males (both at Jodhpur and Ramnagar) may attack and kill infants (Sommer, 1987; Borries, 1997). In

TABLE 5 | Male aggression and displacements directed at females in gray langurs.

	KI group		O group		A group	
Context	***n* Bouts**	**Percentage**	***n* Bouts**	**Percentage**	***n* Bouts**	**Percentage**
Food	23	21.5	86	57.3	16	94.1
Place	2	1.9	10	6.7		
After harassment	2	1.9	7	4.7		
Sexual behavior	4	3.7	4	2.7		
Policing	4	3.7	1	0.7		
Social	7	6.5	8	5.3		
Infant[a]			1	0.7		
Unknown	65	60.7	33	22.0	1	5.9
Total	107	100.0	150	100.0	17	100.0

For context definitions see methods. Observations based on ad libitum and focal animal sampling techniques.
[a]*Single case of a female with a young infant fleeing after a male approached and reached for the infant.*

both populations, more than 30% of infant mortality could be attributed to infanticide committed by males (Borries and Koenig, 2000). Thus, the mainly low intensity of male aggression directed at females in gray langurs does not equal low impact. The sexual conflict between males and females in this species is expressed indirectly *via* attacks on infants and infanticide rather than directly through the sexual coercion of females themselves (see in addition the discussion under section "Contexts of Male Agonism Against Females").

It seems noteworthy that the characterization of despotism extends beyond male-female relationships in gray langurs. At both sites, all agonistic relationships have been characterized as despotic. This is true for male-male relationships at both Jodhpur (Sommer pers. com.) and Ramnagar (Perlman et al., 2016). And it is also true for female-female relationships at Jodhpur (Borries et al., 1991; Lu et al., 2008) and at Ramnagar (Lu et al., 2013; Riaz et al., in preparation). Additionally, the relationship between rank and reproduction for males and females can be characterized as despotic (*sensu* Vehrencamp, 1983), i.e., reproductive skew is high (males Jodhpur: Sommer and Rajpurohit, 1989; males: Ramnagar: Launhardt et al., 2001; females Jodhpur: Borries et al., 1991; females Ramnagar: de Vries et al., 2016). This general despotism in both agonistic relationships and reproductive skew is, however, not the norm among non-human primates. Male and female reproductive skew varies widely in primates (Muller and Emery Thompson, 2012; Pusey, 2012) and may or may not match the dominance style. Even within a single species, male and female dominance styles can differ (Preuschoft et al., 1998).

Do Females Dominate Males and Under Which Circumstances?

We found that aggression by females against males was extremely rare (once every 142–250 h). Furthermore, adult females rarely dominated adult males and the FDI was close to zero. In the few cases when a female had an average dominance index similar to or higher than a male, the respective female never won a single encounter with this male. To some extent this relates to the small sample size in A group, but it also shows that the dominance indices overall are measures of "power" (Hemelrijk et al., 2008) and may not necessarily reflect dyadic relationships.

The finding of rare female aggression against males and few dyads of female dominance over males stands in contrast to the theoretical prediction that depending on the adult sex ratio, females show frequent aggression toward males or females may even dominate some or several males in their group (Hemelrijk et al., 2008, 2020; Izar et al., 2021). So far, such partial female dominance has been shown within some non-human primate species and humans (Stroebe et al., 2017; Hemelrijk et al., 2020; Izar et al., 2021), as well as in a comparative analysis of male-female agonism across a larger sample of non-human primates (Hemelrijk et al., 2008).

An absence of the suggested relationship between partial female dominance and adult sex ratio has previously been found in species with more egalitarian relationships, as in some macaques (Hemelrijk et al., 2008). However, as shown above, gray langurs must be considered despotic in their agonistic relationships and their reproductive skew, making this explanation unlikely.

Another potential reason for the lack of a relationship between partial female dominance and adult sex ratio might relate to prior attributes of fighting ability overriding the suggested winner-loser effects in adult males assumed to facilitate partial female dominance. While the suggested relationship between partial female dominance and adult sex ratio seems to hold across primates and within species such as vervets and capuchins, it might be absent in a single species with very strong sexual size dimorphism. For example, mandrills and gorillas with a body mass dimorphism greater than two have so far not been shown to have partial female dominance (Table 4 in Hemelrijk et al., 2008). However, gray langurs have a body mass dimorphism of about 1.3 (Smith and Jungers, 1997), which is much lower than in gorillas and mandrills. In fact, the dimorphism in gray langurs is even lower than in vervets and capuchins thus also rendering this explanation unlikely.

In addition, a relationship between adult sex ratio and partial female dominance is predicted to occur when conflict levels among males are high. In this situation, the winner-loser effects among males may be stronger and females can benefit from exploiting these effects (Stroebe et al., 2017). In gray langur males at Ramnagar agonism consists of about equal proportions of aggression and submission, and most aggression is

of low intensity (75%; Koenig and Borries, unpublished), perhaps indicating a low level of conflict. This contrasts with the finding that injuries among males are twice as frequent as among females (Feder et al., 2019). Thus, we are not in the position to test the idea of winner-loser effects but contend that a low level of agonistic conflict among males could relate to the absence of an adult sex ratio effect.

It seems noteworthy that, while female aggression against males was rare, it occurred in specific contexts. Interestingly, females (in O group) behaved aggressively most frequently during high stakes interventions, when infants or older offspring were perceived as at risk. During these situations females even formed coalitions with each other, a behavior that is otherwise rare among gray langur females (Borries, 1993). While speculative, because of the few events observed, this might indicate that females may dominate males in specific contexts only, i.e., context-dependent dominance or spheres of dominance (Hand, 1986; Preuschoft and van Schaik, 2000). If true, this could explain why a general dominance index would not yield partial female dominance.

Overall, we note that the proposed relationship between female aggression, partial female dominance, and adult sex ratio does not seem to hold in gray langurs. Our study suggests more variation in these relationships than previously thought (Hemelrijk et al., 2008, 2020). More studies with many more species are clearly needed to determine how general the predicted relationships are and if the expected criteria are being met.

Contexts of Male Agonism Against Females

We found that agonistic behavior of males against females occurred primarily over food but was very rarely observed in a policing or sexual context.

The near absence of male policing as a context of male agonism seems to fit the general primate pattern (Watts et al., 2000). Male interventions are expected to be more common when female dispersal is common. Here, conflicts between females may lead to the loser leaving the group and male interventions may act to calm conflicts, facilitate female integration, and prevent dispersal (Watts et al., 2000). In support of this idea, male interventions seem to be more common in species with female dispersal such as gorillas, hamadryas baboons, and some Asian colobines (Watts et al., 2000). In contrast, female dispersal in gray langurs is extremely rare (Borries et al., 1991; Koenig et al., 1998) and, hence, frequent male intervention is neither expected nor found.

We observed only two cases (in O group) regarding direct sexual coercion that might link sexual behavior and agonism. This does not necessarily mean that male aggression cannot affect the behavior of receptive females, because aggression and mating may be decoupled (Baniel et al., 2017). Gray langur males, at least in Ramnagar, have been shown to vary in their aggressiveness, but high aggressiveness did not lead to higher reproductive success (Borries et al., 2017). In addition, the overall low level of aggression, particularly high intensity aggression, makes it unlikely that direct sexual coercion is a tactic used by gray langur males. These results stand in contrast to the findings of frequent sexual coercion that have accumulated over the past years particularly for some baboons and chimpanzees (Muller et al., 2007, 2009, 2011; Swedell et al., 2014; Baniel et al., 2017; Watts, 2022). Importantly, in these species male aggression not only occurs frequently, but is a tactic that increases mating and reproductive success (Muller et al., 2007, 2011; Feldblum et al., 2014; Baniel et al., 2017; Watts, 2022). However, our results emphasize the need for a broader look at the causes underlying this variation in male reproductive tactics.

Overall, most of the agonistic behavior of males directed at females occurred over access to food. This is insofar surprising as the potential effect of feeding competition is almost never explicitly considered in male-male or male-female relationships (but see Perry, 1997; Pereira et al., 2000; Schuelke, 2001; Muller et al., 2009; Perlman et al., 2016). However, males need appropriate food to stay healthy and to compete with other males (Muller et al., 2009). Importantly, in the study population at Ramnagar, male physical condition is an important aspect relating to male dominance rank; males in better physical condition are often higher ranking (Perlman et al., 2016). It is thus not very surprising that male agonism even toward females centers on food. As male reproductive success is primarily affected by dominance rank (Launhardt et al., 2001) and dominance rank is affected by access to food (Perlman et al., 2016), males may compete with females over food. The importance of feeding competition is further underscored by the fact that agonism over food for male-male dyads was the second most common context with more than 25% (most common was the context unknown; Koenig and Borries, unpublished). In addition, the proportion of intersexual conflicts over food is very similar to female-female dyads, where it ranged between 50 and 80% (Koenig and Borries, 2006). Unfortunately, there are very little comparative data available for male-female agonism. In some primate species, food context may make up around 20% of male-female conflicts (Smuts, 1987; Muller et al., 2009) and only some species of capuchins have more frequent encounters over food (Janson, 1985; O'Brien, 1991). The latter fits with other observations of capuchins, in which foraging of females was frequently interrupted by males and females formed coalitions to supplant males from feeding sites (Rose, 1994; Perry, 1997). Thus, while this topic has received little attention, the few available results suggest that competition for food can be an important factor impacting male-female relationships.

Overall, our results indicate that female gray langurs may face not one but two major costs of living in groups with males. They face the threat of infanticide, and also compete with males over access to food. While we know that infanticide has a significant impact on female fitness, the effect of intersexual feeding competition is less clear and requires further study.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the two non-invasive studies were conducted in 1985 (in India) and 1994-95 (in Nepal), respectively.

AUTHOR CONTRIBUTIONS

AK and CB collected and analyzed the data from Ramnagar, Nepal, and Jodhpur, India, respectively, and designed this study. AM and DR transcribed and proofread the data, ran first analyses, and produced first tables, with assisted by AK and CB. AK drafted the manuscript. All authors contributed to and edited the content, structure, and language.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.860437/full#supplementary-material

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Evaluating drivers of female dominance in the spotted hyena

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Introduction: Dominance relationships in which females dominate males are rare among mammals. Mechanistic hypotheses explaining the occurrence of female dominance suggest that females dominate males because (1) they are intrinsically more aggressive or less submissive than males, and/or (2) they have access to more social support than males.

Methods: Here, we examine the determinants of female dominance across ontogenetic development in spotted hyenas (*Crocuta crocuta*) using 30 years of detailed behavioral observations from the Mara Hyena Project to evaluate these two hypotheses.

Results: Among adult hyenas, we find that females spontaneously aggress at higher rates than males, whereas males spontaneously submit at higher rates than females. Once an aggressive interaction has been initiated, adult females are more likely than immigrant males to elicit submission from members of the opposite sex, and both adult natal and immigrant males are more likely than adult females to offer submission in response to an aggressive act. We also find that adult male aggressors are more likely to receive social support than are adult female aggressors, and that both adult natal and immigrant males are 2–3 times more likely to receive support when attacking a female than when attacking another male. Across all age classes, females are more likely than males to be targets of aggressive acts that occur with support. Further, receiving social support does slightly help immigrant males elicit submission from adult females compared to immigrant males acting alone, and it also helps females elicit submission from other females. However, adult females can dominate immigrant males with or without support far more often than immigrant males can dominate females, even when the immigrants are supported against females.

Discussion: Overall, we find evidence for both mechanisms hypothesized to mediate female dominance in this species: (1) male and female hyenas clearly differ in their aggressive and submissive tendencies, and (2) realized social support plays an important role in shaping dominance relationships within a clan. Nevertheless, our results suggest that social

support alone cannot explain sex-biased dominance in spotted hyenas. Although realized social support can certainly influence fight outcomes among females, adult females can easily dominate immigrant males without any support at all.

KEYWORDS

dominance, intrinsic sex differences, social support, aggressive behavior, submissive behavior

Introduction

Dominance hierarchies are common in animal societies and have profound fitness consequences for individuals of many different species (Strauss et al., 2022). Interestingly, in some animals, one sex is typically dominant over the other, prompting questions about the evolutionary and mechanistic origins of this sex bias. Male dominance, where males exert power or influence over females, is very common in mammals and has thus been studied extensively (Carpenter, 1942; Darwin et al., 1981; Drews, 1993). A diverse array of traits facilitates male dominance, including larger body size (Cassini, 2020), superior weaponry (Rico-Guevara and Hurme, 2019), higher androgen concentrations (Nelson, 2005), and more frequent and intense expression of aggressive behavior (Nelson, 2005). These sexually dimorphic, male-biased traits are often correlated (e.g., male aggression levels and circulating testosterone; Muller, 2017), and in most cases, they provide an advantage in both intra- and inter-sexual competition (Nelson, 2005).

Female dominance, where females exert power or influence over males, is uncommon in mammals but occurs in various Malagasy primates (Lewis, 2020), two species of mole rats (*Cryptomys hottentotus* and *Heterocephalus glaber*; Holekamp and Engh, 2009), and spotted hyenas (*Crocuta crocuta*; Kruuk, 1972). Compared to the factors influencing male dominance, those that mediate female dominance in mammalian societies remain poorly understood. Nevertheless, three proximate mechanisms leading to female dominance over males have been proposed: (1) intrinsic attributes or sex-based differences in the ability to use force (e.g., body size, physical strength, aggressiveness; Watts et al., 2009); (2) extrinsic, or derived, attributes, including sex-based differences in social support (e.g., coalition and alliance partners; Vullioud et al., 2019), and (3) leverage or sex-based differences in resources that cannot be taken by force (e.g., fertilizable eggs; Lewis, 2020).

Spotted hyenas offer an ideal system in which to examine the phenomenon of female dominance, as adult female dominance over adult males has been consistently observed in this species. Given that hyenas are a gregarious species, it is also possible to use them to test some of the hypotheses identified above (Kruuk, 1972; East et al., 2003; Holekamp and Strauss, 2020). Spotted hyenas live in mixed-sex matrilineal societies called 'clans,' which are characterized by low within-group relatedness, female philopatry, and male dispersal (Smale et al., 1997; Van Horn et al., 2004; Holekamp et al., 2012). Past studies of spotted hyenas have supported both the intrinsic attributes hypothesis (Frank, 1986) and the social support hypothesis (Vullioud et al., 2019).

Although we were unable to assess the leverage hypothesis in this study, we examined both the intrinsic attributes hypothesis and the social support hypothesis. According to our interpretation of the intrinsic attributes hypothesis, behavioral and physiological differences between the sexes contribute to female dominance in hyenas. Under this hypothesis, females have enhanced fighting abilities due to selection favoring females who can obtain priority of access to resources for themselves or their offspring (Watts et al., 2009; Clutton-Brock and Huchard, 2013), and these abilities then support females in achieving intersexual dominance. As adults, female-spotted hyenas aggress at higher rates and intensities than immigrant males when attacking lower-ranking hyenas (McCormick et al., 2021). Additionally, more aggressive behavior is associated with superior reproductive success among females (Watts et al., 2009; Yoshida et al., 2016; McCormick and Holekamp, 2022) but not among male spotted hyenas (East and Hofer, 2001). This suggests that aggressiveness may be selected for in females, but not necessarily in males, and this could give females an edge over males in contests of dominance. In further support of this hypothesis, sex differences in aggressive behavior in spotted hyenas emerge early in life during the neonatal period (Smale et al., 1995; Golla et al., 1999; Wahaj and Holekamp, 2006; Benhaiem et al., 2012).

The social support hypothesis suggests that differential social support allows females to dominate males (Vullioud et al., 2019). Under this hypothesis, female dominance over adult males arises because females have more social support than males, driven by male-biased dispersal that leads adult males to join a new clan where they lack kinship or social ties. Consistent with this hypothesis, Vullioud et al. (2019) found that the outcomes of dyadic interactions between spotted hyenas in Ngorongoro Crater, Tanzania, were better predicted by a proxy for social support than by the sexes of the fight contestants

or the differences between them in body size. In this study, social support was approximated by an algorithm that used a combination of kinship, dispersal status, maternal pedigree, and physical location relative to the center of each hyena's home range to estimate which of the contestants was more likely to receive social support from other hyenas that could potentially arrive during the agonistic encounter. Additional support for this hypothesis comes from work demonstrating that support from social allies during agonistic encounters aids in rank acquisition (Engh et al., 2000) and facilitates rank reversals among adult females (Strauss and Holekamp, 2019).

Here, we interrogated both the intrinsic attributes hypothesis and the social support hypothesis in explaining the tendency for females to dominate males among spotted hyenas. Although these hypotheses are not mutually exclusive, they are often characterized as being in conflict (e.g., Vullioud et al., 2019), despite the aforementioned evidence supporting both hypotheses. Here, we clarified the contributions of these different mechanisms to female-biased dominance using a 30-year dataset on spotted hyenas in Kenya. Regarding the intrinsic attributes hypothesis, we added to the work of McCormick et al. (2021) by investigating unsolicited aggressive and submissive behavior across age and sex classes. Regarding the social support hypothesis, we added to the work of Vullioud et al. (2019) on the potential for receiving social support by investigating realized social support during both successful and unsuccessful spontaneous agonistic behavior.

To test the predictions of both hypothesized mechanisms, we focused initially on agonistic interactions among adult hyenas, where female dominance is most clearly expressed. We examined four aspects of agonistic interactions: (1) the initiation of agonistic interactions by producing spontaneous aggressive or submissive behaviors, (2) the propensity for aggressive acts to be successful, as indicated by eliciting submission from the target animal (e.g., successfully dominating the recipient of the aggression), (3) the likelihood of receiving social support during an aggressive act, and (4) in opposite-sex group-mates, the effect of realized social support on the success of aggression in eliciting a submissive response from the targeted animal. Predictions made by the two hypotheses about these four aspects of agonistic interactions are presented in **Table 1**. Notably, the two hypotheses make contrasting predictions about the behavior of adult natal males. The intrinsic attributes hypothesis predicts that natal males should behave more similarly to immigrant males than females because of intrinsic sex differences in adult hyenas, whereas the social support hypothesis predicts that natal males should behave more similarly to females than immigrant males because of the greater potential for receiving social support enjoyed by natal individuals (Vullioud et al., 2019; **Table 1**). **Table 1** also presents two additional predictions that follow from the hypothesis that social support is a primary driver of sex differences in dominance in hyenas: (1) natal males and females should receive more social support than immigrant males and (2) receiving social support should help females and natal males successfully elicit submission from immigrant males. After testing these hypotheses in adults, we considered an ontogenetic perspective by examining determinants of female-biased dominance in hyenas that were yet to reach adulthood.

Materials and methods

Study species

Female spotted hyenas invest heavily in the rearing of offspring (East et al., 2009; Watts et al., 2009; Laubach et al., 2021). They usually bear litters of 1 or 2 cubs; when twin cubs are born, neonatal females dominate males in 67–84% of mixed-sex twin litters (Smale et al., 1995; Golla et al., 1999; Wahaj and Holekamp, 2006; Benhaiem et al., 2012). During the first 2 years of life, juveniles of both sexes assume the social ranks and entire social networks of their mothers (Smale et al., 1993; Holekamp and Smale, 1998; Strauss et al., 2020; Ilany et al., 2021). Young animals of both sexes generally retain their maternal rank as long as they remain in the natal clan, resulting, on average, in parity between the sexes with respect to dominance rank among cubs and subadults. Full-blown female dominance over males emerges after reproductive maturity and male dispersal.

One to 6 years after becoming reproductively mature, most male spotted hyenas disperse to join new social groups (Smale et al., 1997; Höner et al., 2007), a process that induces a suite of physiological, behavioral, and social changes (Holekamp and Sisk, 2003). It also generates two classes of adult males in most hyena clans: immigrant males who have arrived from other clans and adult natal males who have not yet dispersed. In the context of the matrilineal hierarchy, immigrant males are lower ranking than all females and natal males in the group (East and Hofer, 2001); however, immigrant males have been found to sire the vast majority of offspring within our study system (Engh et al., 2002; Van Horn et al., 2004). Immigration into a new clan by a male spotted hyena coincides with an increase in the frequency with which he exhibits extreme submissive behavior (Smale et al., 1997); it also coincides with an elevation in circulating testosterone concentrations and onset of adult testicular function (Holekamp and Sisk, 2003; Curren et al., 2013). Finally, by joining a new group of unfamiliar conspecifics, dispersing males not only experience a drastic decline in their priority of access to food resources (Smale et al., 1997) but they also lose most or all of their established social relationships (Vullioud et al., 2019).

Study population

In this study, we used data collected between 1988 and 2018 from three clans of spotted hyenas inhabiting the Maasai Mara

TABLE 1 Predictions at different stages of agonistic interaction made by the two hypotheses under investigation, with symbols indicating whether results from this study support (+), fail to support (−), or show mixed support (~) for each prediction.

Stage of agonistic interaction	Prediction				Figure
	Intrinsic attributes hypothesis		Social support hypothesis		
Initiation of agonistic interactions	Females produce unsolicited aggression at higher rates than natal and immigrant males	+	Natal males and females produce unsolicited aggression at higher rates than immigrant males	−	Figure 1
	Immigrant and natal males produce unsolicited submission at higher rates than females	+	Immigrant males initiate interactions with submission at higher rates than do natal males or females	−	Figure 2
Outcome of aggressive interactions	Aggression by females is more successful at eliciting submission than aggression by natal or immigrant males	−	Aggression by natal males and females is more successful at eliciting submission than aggression by immigrant males	~	Figure 3A
	Natal and immigrant males are more likely than females to offer submission to an aggressor	+	Immigrant males are more likely than natal males or females to offer submission to an aggressor	−	Figure 3B
Receipt of social support			Females and natal males receive support at higher rates than immigrant males	−	Figure 4A
Effect of realized social support			Receiving social support helps females and natal males dominate immigrant males	−	Figure 5

National Reserve, Kenya. Individual hyenas were identified by their unique spots and other marks, such as scars and ear damage. The sex of each individual was determined based on the shape of the glans of its erect phallus (Frank et al., 1990), and ages of natal animals were determined to ± 7 days based on cub appearance when first seen (Holekamp et al., 1996). We classified hyenas in their first year of life as cubs; these individuals are largely dependent on their mothers for food and on communal dens for refugia (Holekamp and Smale, 1998). These communal dens differ from natal dens, where female hyenas give birth and rear offspring for the first 2–5 weeks of life in seclusion (East et al., 1989; Boydston et al., 2006). We classified hyenas in their second year of life as subadults; these individuals are weaned on average at 13 months, and they no longer use communal dens but remain heavily dependent on their mothers for access to food and protection (Watts et al., 2009). We classified hyenas of 2 years and older as adults; hyenas of both sexes are physiologically able to breed at 2 years (Glickman et al., 1992). As a result, there are three categories of resident adult hyenas within each clan: females, natal males that have not yet dispersed, and immigrant males that have successfully left their natal clan to join a new one. Here, a dispersing adult male was considered to have successfully immigrated into a new clan after he was observed in the clan's territory for at least 6 months and observed interacting with clan residents at least 3 times (Engh et al., 2002). In this population, 59.8% (SD = 15.4%) of adult males are immigrants.

Observations were made daily from vehicles for 3–4 h around dawn and again around dusk. We defined an observation session as observing 1 or more hyenas separated from others by at least 200 m (Holekamp et al., 1997; Yoshida et al., 2016). In each session, we identified all hyenas present, and we used all-occurrence sampling (Altmann, 1974) to record all acts of aggressive and submissive behavior and the responses to these acts. Such acts were considered unsolicited (spontaneous) if they were not immediately preceded by a prior aggressive act. We restricted our analyses to observation sessions in which 2 or more hyenas were present, and we excluded observation sessions that occurred at natal dens, as mothers typically hide natal dens well and minimize interactions with clan mates. We also excluded sessions under 10 min, as these sessions comprised mostly observations of inactive or sleeping hyenas.

Social ranks were assigned yearly based on wins and losses in agonistic encounters between individuals within the study groups. For each year, individual ranks from the prior year were updated based on the outcomes of observed agonistic encounters in that year. Individuals under the age of 13 months at the start of the year were assigned their mother's rank (Strauss et al., 2020). Individuals first joining the group or first becoming old enough to have ranks calculated were assigned an initial rank based on their arrival and tenure in the clan (for immigrants; East and Hofer, 2001) or their mother's rank (for natal individuals); the initial rank was then updated based on observed agonistic interactions during that year (Strauss and Holekamp, 2019). To account for the variation in group size, rank was standardized within each year to range from -1 to 1.

Calculating rates of unsolicited aggressive and submissive behaviors

To assess rates of unsolicited aggressive and submissive behavior, we counted the number of aggressive or submissive acts emitted by each individual present in each observation

session. These included observation sessions where individuals were typically active within the observation period but did not direct any unsolicited aggressive or submissive acts toward other hyenas present, therefore resulting in a count of zero within the observation session. Aggressive behaviors included intention movements to attack, threats, attack behaviors without bodily contact, and physical contact that might result in injury. Submissive behaviors included appeasement signals such as flattening the ears back against the head or head-bobbing, postural changes such as folding the entire body into a submissive posture with tail down between the legs, and "groveling," or crawling on one's belly and carpals (Kruuk, 1972). Descriptions of all agonistic behaviors in our dataset can be found in **Supplementary material**. Regarding aggressive behavior, we only included acts of spontaneous aggression and did not count acts of aggression that were immediate responses to a prior aggressive act directed at the focal individual, such as counterattacks (n = 861 of 80,597 aggressive acts, or 1.07%). Regarding unsolicited submissive behavior, we only included spontaneous submissive acts that were emitted in the absence of an immediately preceding aggressive act directed at the focal animal.

Calculating dominance

An individual was considered to successfully dominate another individual during an agonistic encounter if the recipient of an aggressive act emitted a submissive response. This resulted in a binary variable, successful vs. unsuccessful aggressive acts, indicating whether or not the recipient hyena emitted a submissive response to a threat or attack. It should be noted that, if a recipient did not respond with submissive behavior, it did not necessarily mean that the aggressor was dominated; instead, it simply meant that the threat was not successful in eliciting a submission from the recipient.

Calculating realized social support

An individual was considered to have been supported during an agonistic interaction if another hyena present during an observation session either acted simultaneously with it to attack the target animal or joined in an ongoing attack. This resulted in a binary factor, supported vs. unsupported aggression, indicating whether or not the aggressor received support from 1 or more clan mates during an agonistic encounter. We used this binary variable of realized social support to assess sex differences in the likelihood of receiving social support during an agonistic encounter and to assess the effect of realized social support on dominance. If both individuals attacked a target animal simultaneously, both were considered supported actors, and each was included as a separate observation in the dataset. Individuals that joined after the initial act of aggression were not included as actors in the dataset, as these joining individuals were not initiators of the conflict.

Modeling rates of aggression and submission

To compare variation in spontaneous aggressive and submissive behavior between sexes and among stages of ontogeny, we built separate mixed models for each age class (cubs, subadults, adults) that included the sex of the acting individual ("actor") as the independent variable and counts of aggressive and submissive behaviors as the dependent variables. Note that for all adult models we had three categorical variables for actor and recipient sexes: adult female, adult natal male, and adult immigrant male. The number of hyenas present in the observation session was included as a covariate to control for opportunities to interact and known effects of group size on rates of social behavior (McCormick and Holekamp, 2022). The standardized rank of the actor was also included as a covariate to control for known effects of social rank on dominance behavior (McCormick and Holekamp, 2022). The duration of the observation session in minutes was included as a log offset to account for individual variation in the time observed. The observation session ID was included as a random intercept to account for non-independence of measurements within sessions, and actor ID was included as a random intercept to account for non-independence of measurements of individual variation in aggressive behavior.

Models were built using a zero-inflated Poisson approach within the glmmTMB package in R (Brooks et al., 2017), and we reported estimated incidence rate ratios (IRR) in which we set females as the reference group. These IRR values are calculated from exponentiating the model estimates comparing males to the female reference category, such that an IRR of 2 would be interpreted as males exhibiting the modeled behavior 2 times more often than females.

Modeling dominance and realized social support

To ascertain whether successfully dominating another group member was driven by the sex of the actor or the sex of the recipient, we built logistic regression models including actor sex and recipient sex as independent variables and dominance (successful vs. unsuccessful act of aggression)

as the binary dependent variable. This allowed for both intra- and inter-sexual comparisons of whether or not an aggressive act elicited a submissive response. We included an interaction term in our models to test whether the effect of actor sex on dominance depends on recipient sex and vice versa. As random intercepts, we included an observation session ID (see above) and a dyad ID of paired actors and recipients, to account for repeated interactions between the same individuals.

To assess whether members of one sex received more social support than members of the other sex, we built logistic regression models that included actor sex and recipient sex as independent variables and realized support (supported vs. unsupported act of aggression) as the binary dependent variable. We again included an interaction between actor sex and recipient sex as a fixed effect, as well as observation session ID and dyad ID as random intercepts.

To determine whether realized social support during an agonistic encounter affected the supported hyena's ability to successfully dominate a member of the opposite sex, we built logistic regression models that included actor sex, recipient sex, and realized support (supported vs. unsupported act of aggression) as independent variables and dominance (successful vs. unsuccessful act of aggression) as the binary dependent variable. We also included a three-way interaction between actor sex, recipient sex, and support, as well as observation session ID and dyad ID as random intercepts.

To address our research questions, we built a separate mixed model for each actor age class (adults, subadults, and cubs) to compare the effect of sex on dominance and realized social support throughout ontogeny. Aggressive acts were separated by actor age and filtered to require actors to aggress upon individuals of their own or older age classes; for example, the subadult model included subadult actors and both subadult and adult recipients. All models for dominance and realized social support were logistic regression models fit using the glmer function in the lme4 package (Bates et al., 2015). If we found a significant interaction between any explanatory variables at $\alpha = 0.05$, we further stratified our analyses based on both actor sex and recipient sex to assess their joint effects on, dominance, and realized social support.

All models were built using R software (R Core Team, 2021). All models were tested for violations of dispersion, within-group deviation of uniformity, homogeneity of variance (Levene Test), and influence of outliers using the DHARMa package (Hartig and Lohse, 2022). The inclusion of relevant random intercepts was checked by calculating the intraclass correlation coefficients (ICCs). If a random intercept did not account for a sufficient variation in the model (ICC < 0.1), then it was dropped. Finally, all models were assessed using two-tailed tests with an alpha set at 0.05.

Results

Initiation of agonistic interactions

Spontaneous aggressive behavior

Among adults, comparisons of incidence rate ratios (IRRs) revealed that both adult immigrant males (IRR = 0.551; 95% CI = 0.482, 0.633, $p < 0.001$; **Figure 1**), and adult natal males (IRR = 0.644; 95% CI = 0.568, 0.729; $p < 0.001$; **Figure 1**) emitted spontaneous aggressive acts at approximately half the rate of adult females. We found no sex difference in aggression rates among either cubs (IRR = 0.890; 95% CI = 0.729, 1.085; $p = 0.249$; **Figure 1**) or subadults (IRR = 1.034; 95% CI = 0.891, 1.199; $p = 0.482$; **Figure 1**). Here, we used 103,063 observations of 305 females across the three age classes, 370 natal males across the three age classes, and 152 adult immigrant males to compare sex differences in aggressive behavior. A summary of the data for counts of spontaneous aggressive behaviors can be found in **Supplementary Table 1**.

Spontaneous submissive behavior

Among adults, adult immigrant males emitted spontaneous acts of submission roughly 60% more often than did adult females (IRR = 1.611; 95% CI = 1.388, 1.872; $p < 0.001$; **Figure 2**), and adult natal males roughly 70% more often than adult females (IRR = 1.708; 95% CI = 1.499, 1.946; $p < 0.001$; **Figure 2**). We found no sex difference in submission rates among either cubs (IRR = 0.897; 95% CI = 0.740, 1.086; $p = 0.265$; **Figure 2**) or subadults (IRR = 0.982; 95% CI = 0.799, 1.208; $p = 0.866$; **Figure 2**). Here, we used 81,681 observations of 316 females across the three age classes, 366 natal males across the three age classes, and 156 adult immigrant males. A summary of the data for counts of spontaneous submissive behaviors can be found in **Supplementary Table 1**.

Outcome of aggressive interactions

A summary of the number of acting individuals broken down by sex and age class for the following models of aggressive interactions and support can be found in **Supplementary Table 2**. In our initial model of dominance (successful vs. unsuccessful act of aggression), we found a significant interaction between actor sex and recipient sex in the model for adults (**Supplementary Figure 1** and **Supplementary Table 3**). Given the significant interaction, we assessed the effect of actor sex on dominance while stratifying on recipient sex, and we assessed the effect of recipient sex on dominance while stratifying on actor sex. For consistency, we replicated this stratified model structure for cubs and subadults as well. Here, and in all remaining models, we used 79,736

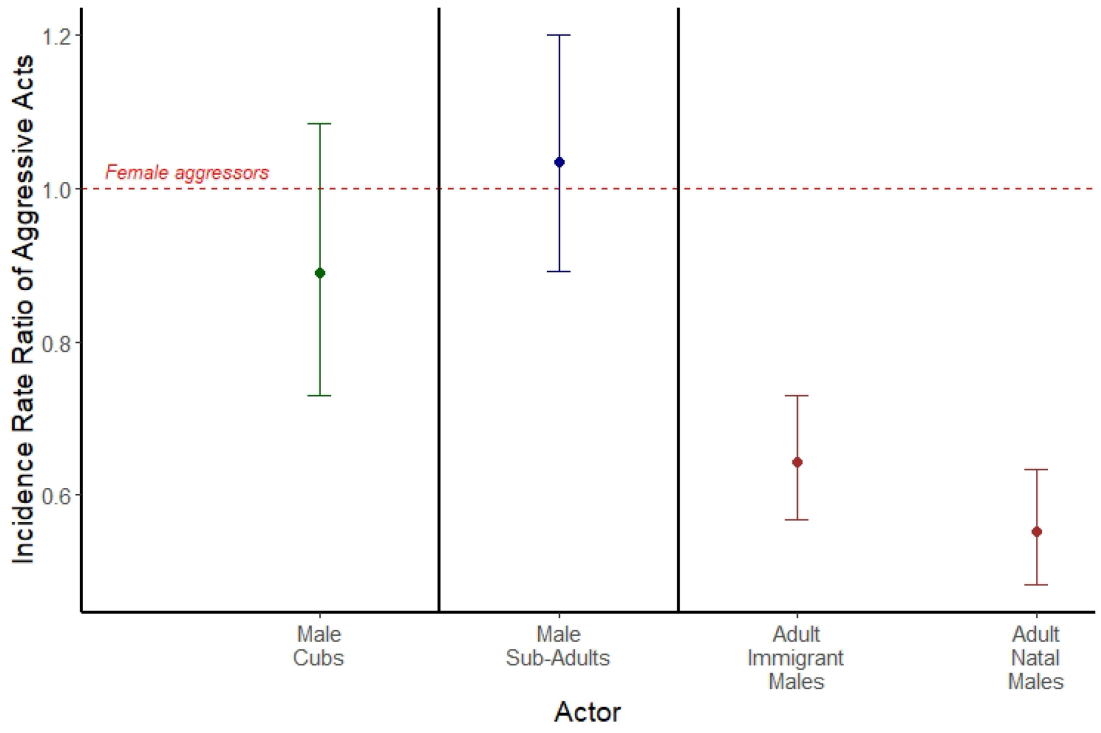

FIGURE 1
Incidence rate ratios of spontaneous aggressive acts emitted by male cubs (green), male subadults (blue), adult immigrant males (brown), and adult natal males (brown). Each is compared to a female aggressor reference group of the same age class, represented by the red dashed line. Points represent the estimated incidence rate ratios from three separate mixed models separated by bold black lines (actors who are cubs, actors who are subadults, and actors who are adults), and error bars represent 95% confidence intervals around the incidence rate ratio.

observations of 366 females across the three age classes, 410 natal males across the three age classes, and 219 adult immigrant males.

Eliciting submission

In our models stratified by recipient sex (**Figure 3A** and **Supplementary Table 4**), we investigated the effect of actor sex on the odds of an actor eliciting a submissive response. Among adults, when recipients were females, adult immigrant male actors were considerably less likely than adult female actors to elicit a submissive response (OR = 0.122; 95% CI = 0.083, 0.179; $p < 0.001$; **Figure 3A**), but adult natal male actors were just as likely as adult female actors to elicit a submissive response (OR = 0.875; 95% CI = 0.674, 1.136; $p = 0.317$; **Figure 3A**). Adult immigrant males, adult natal males, and adult females initiating an aggressive act were equally likely to receive a submissive response from either immigrant or natal male recipients (**Figure 3A** and **Supplementary Table 4**). In both cubs and subadults, males and females initiating an aggressive act were equally likely to receive a submissive response from recipients regardless of recipient sex (**Figure 3A** and **Supplementary Table 4**).

Offering submission in response to aggressive acts

In our models stratified by actor sex (**Figure 3B** and **Supplementary Table 5**), we investigated the effect of recipient sex on the odds of the recipient responding with submissive behavior. Among adults, when the aggressors were females, both adult immigrant male recipients (OR = 1.831; 95% CI = 1.589, 2.108; $p < 0.001$) and adult natal male recipients (OR = 2.207; 95% CI = 1.197, 4.067; $p = 0.011$) were more likely to submit than adult female recipients (**Figure 3B**). When adult immigrant males were the aggressors, both adult immigrant male recipients (OR = 10.536; 95% CI = 4.719, 23.520; $p < 0.001$) and adult natal male recipients (OR = 4.607; 95% CI = 1.355, 15.664; $p = 0.014$) were more likely to submit than adult female recipients (**Figure 3B**). When adult natal males were the aggressors, both sexes were equally likely to offer a submissive response (**Figure 3B** and **Supplementary Table 5**).

Among subadults, recipient sex was not associated with a difference in offering submission: male recipients were just as likely as female recipients to offer a submissive response to both female aggressors and male aggressors (**Figure 3B** and **Supplementary Table 5**). Among cubs, male

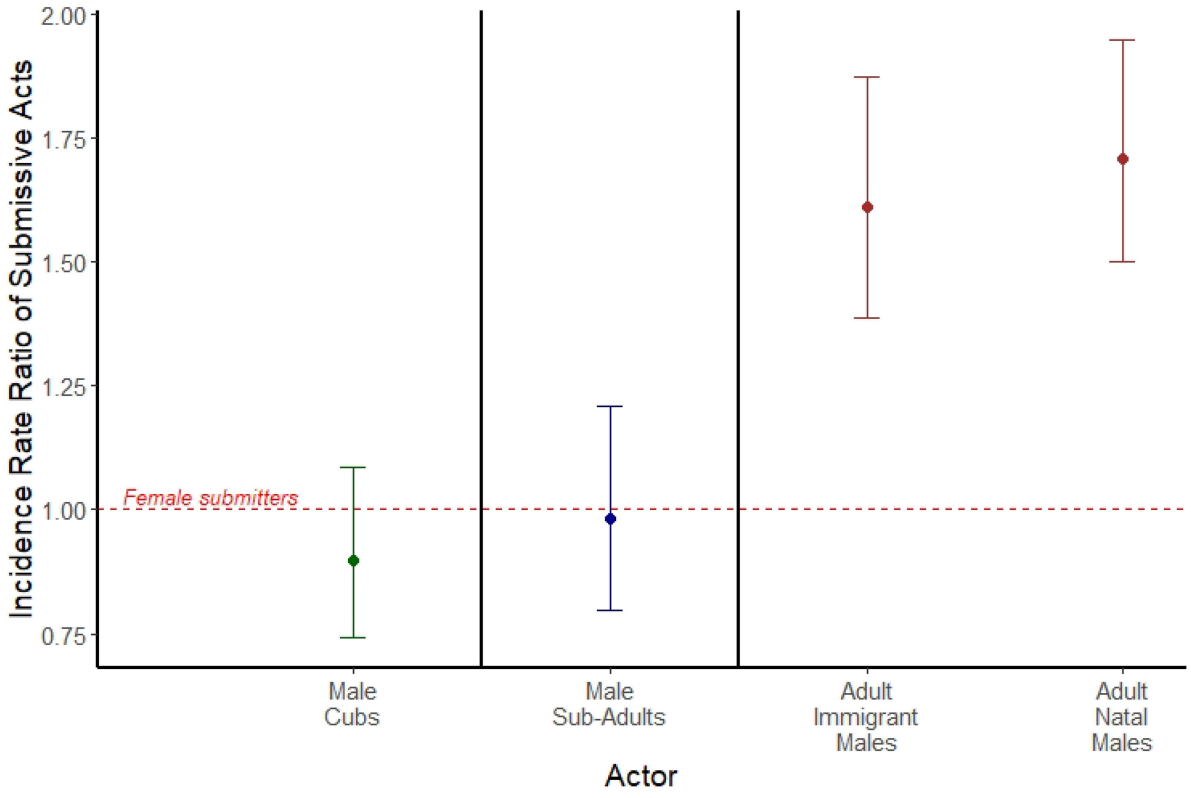

FIGURE 2
Incidence rate ratios of spontaneous submissive acts emitted by male cubs (green), male subadults (blue), adult immigrant males (brown), and adult natal males (brown). Each is compared to a female actor reference group of the same age class, represented by the red dashed line. Points represent the estimated incidence rate ratios from three separate mixed models separated by bold black lines (actors who are cubs, actors who are subadults, and actors who are adults), and error bars represent 95% confidence intervals around the incidence rate ratio.

recipients were more likely than female recipients to offer a submissive response to both female aggressors (OR = 1.461; 95% CI = 1.190, 1.795; $p < 0.001$; Figure 3B) and male aggressors (OR = 2.255; 95% CI = 1.504, 3.381; $p < 0.001$; Figure 3B).

Receipt of social support

Next, we inquired whether there were sex differences in receiving social support or being targeted by coalitionary social support during spontaneous aggressive acts. In our initial models of realized social support (supported vs. unsupported act of aggression), there was no significant interaction between actor sex and recipient sex in any models across the three age classes (cub, subadult, and adult), so the interaction term was not included in the final models and main effects were reported (Supplementary Figure 2 and Supplementary Table 6). A summary of the number of acting individuals broken down by sex, age class, and support can be found in Supplementary Table 2. For consistency with prior results, we stratified our models on actor sex and recipient sex to report and display odds ratios of the effects of actor sex and recipient sex separately.

Receiving social support

Among adult actors, we found that both adult immigrant males (OR = 3.606; 95% CI = 2.990, 4.340; $p < 0.001$) and adult natal males (OR = 2.565; 95% CI = 2.147, 3.065; $p < 0.001$) were 2–3 times more likely than adult females to receive social support during aggressive interactions (Figure 4A). Male and female actors were equally likely to receive social support during attacks among both cubs (OR = 1.010; 95% CI = 0.857, 1.190; $p = 0.906$) and subadults (OR = 1.120; 95% CI = 0.935, 1.330; $p = 0.223$; Figure 4A).

Being targeted by socially supported aggressors

In all age classes, females were more likely than males to be the targets of aggression when actors were supported (Figure 4B). Among adult recipients, both adult immigrant males (OR = 0.211; 95% CI = 0.186, 0.239; $p < 0.001$) and adult natal males (OR = 0.281; 95% CI = 0.203, 0.389; $p < 0.001$) were

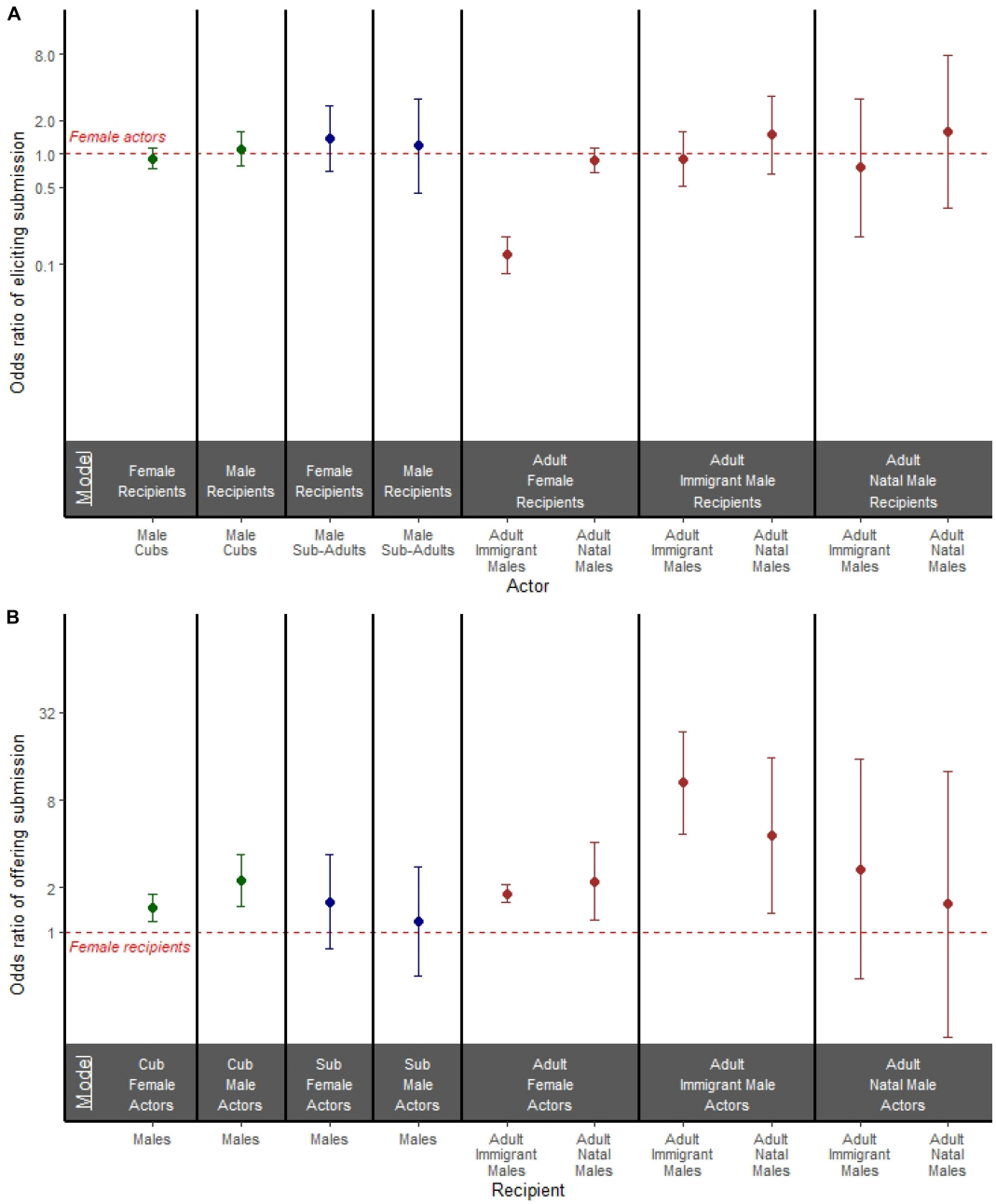

FIGURE 3
(A) Odds ratio of an actor eliciting a submissive response in models stratified by both actor age and recipient sex. **(B)** Odds ratio of a recipient offering a submissive response to aggression in models stratified by both actor age and actor sex. **(A,B)** Models are separated by bold black lines, and age is depicted by color where cubs are green, subadults are blue, and adults are brown. Points represent the odds ratio and error bars represent 95% confidence intervals around the odds ratio. Each point is compared to a female reference group of the same age class represented by the red dashed line.

less likely than adult females to be targets of socially supported aggressors (Figure 4B). Male recipients were also less likely than females to be targets of socially supported aggressors among both cubs (OR = 0.271; 95% CI = 0.226, 0.323; $p < 0.001$; Figure 4B) and subadults (OR = 0.301; 95% CI = 0.247, 0.367; $p < 0.001$; Figure 4B).

Effect of realized social support

Finally, we inquired whether realized social support during an aggressive encounter was associated with dominance outcomes. In our initial model of dominance (successful vs. unsuccessful act of aggression), we found a significant three-way

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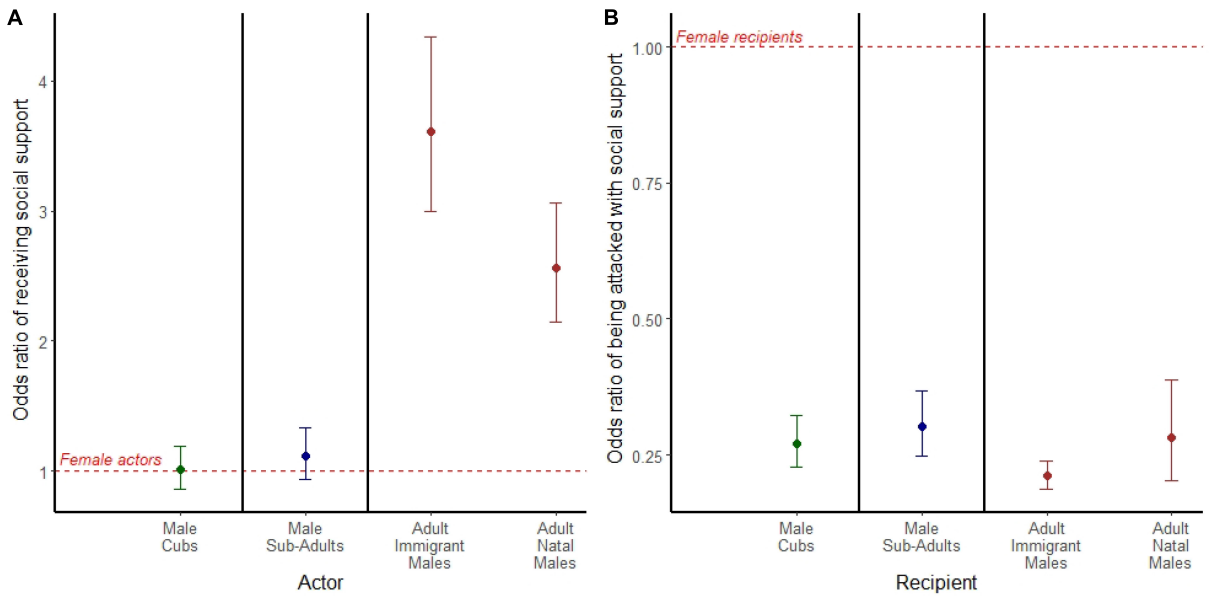

FIGURE 4
(A) Odds ratio of the acting aggressor receiving social support in aggression. **(B)** Odds ratio of an individual being targeted by an actor with social support. **(A,B)** Models are separated by bold black lines, and age is depicted by color where cubs are green, subadults are blue, and adults are brown. Points represent the odds ratio and error bars represent 95% confidence intervals around the odds ratio. Each point is compared to a female reference group of the same age class represented by the red dashed line.

interaction between actor sex, recipient sex, and realized social support in the model for adults (Supplementary Figure 3 and Supplementary Table 7). Given the significant interaction, we stratified the data by both actor sex and recipient sex to assess the effect of realized social support on whether or not an actor was successful in a dominance interaction with a recipient of the opposite sex. For consistency, we replicated this stratified model structure for our models of cubs and subadults as well. A summary of the number of acting individuals broken down by sex and age class for the following models can be found in Supplementary Table 2. In these results and figures, the reference group is unsupported actors, such that each model compares supported vs. unsupported actors of the same sex and age class. We report inter-sex comparisons of the effect of realized social support on dominance outcomes in Figure 5 and in the text below, and we report all other comparisons in Supplementary Table 8.

Among adults, we found that support had no effect on how likely adult immigrant males (OR = 1.954; 95% CI = 0.778, 4.906; p = 0.153) or adult natal males (OR = 1.789; 95% CI = 0.776, 4.123; p = 0.171) were to elicit a submissive response from adult females (Figure 5). Interestingly, supported adult females were actually less likely than unsupported adult females to elicit submissive responses from adult immigrant males (OR = 0.629; 95% CI = 0.441, 0.897; p = 0.011; Figure 5). When adult females aggressed on adult natal males, there was no effect of support on the outcome of the aggression (OR = 0.361; 95% CI = 0.023, 5.432; p = 0.461; Figure 5). Among subadult aggressors, supported subadult males were more likely than unsupported subadult males to elicit submissive responses from female recipients (OR = 5.050; 95% CI = 2.145, 11.886; $p < 0.001$), but support had no effect on the odds of subadult females eliciting a submissive response from males (OR = 0.374; 95% CI = 0.122, 1.147; p = 0.086; Figure 5). Finally, among cubs, there was no effect of support on the odds of male aggressors eliciting a submissive response from females (OR = 1.101; 95% CI = 0.726, 1.670; p = 0.651), or on the odds of female aggressors eliciting a submissive response from males (OR = 1.377; 95% CI = 0.798, 2.373; p = 0.250; Figure 5).

Discussion

Here, we evaluated intrinsic attributes and social support as two non-mutually exclusive hypotheses explaining sex-biased dominance in spotted hyenas. Our results failed to unequivocally support either hypothesis alone, but instead, we found evidence implicating both mechanisms in sex-biased dominance in this species.

Our analysis of unsolicited aggressive and submissive behavior supports the intrinsic attributes hypothesis. We found that, without provocation, adult females were more aggressive than both natal and immigrant adult males (Figure 1), and that both types of adult males were more submissive than adult females (Figure 2). Among cub and subadult hyenas,

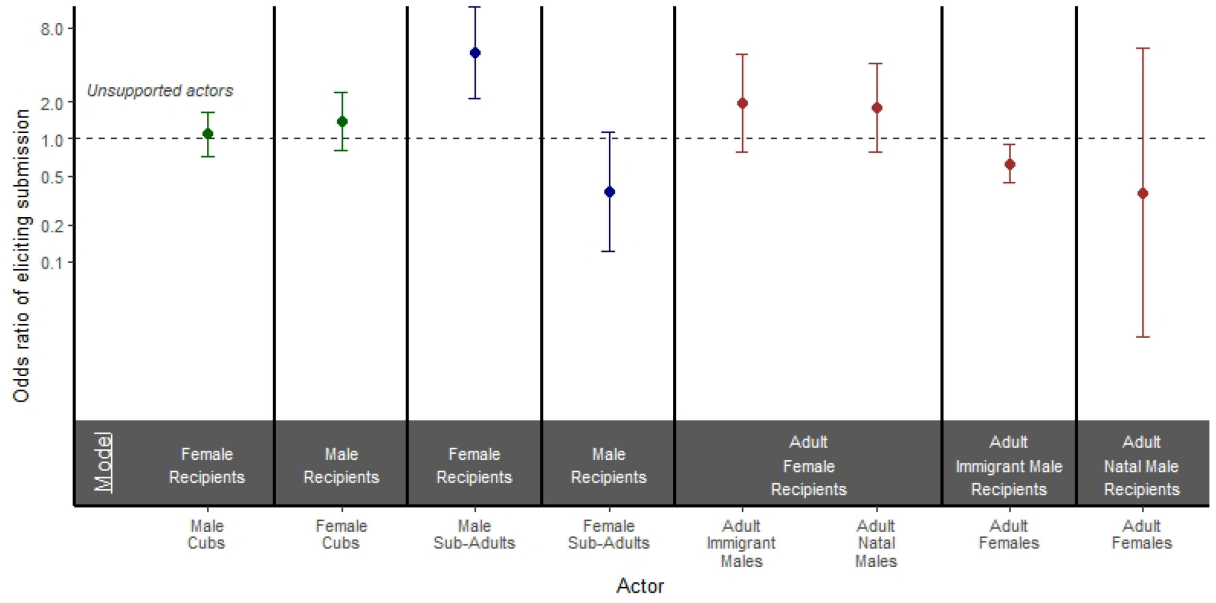

FIGURE 5
Odds ratio of a supported versus unsupported actor eliciting a submissive response from a recipient of the opposite sex in models stratified by both actor age and actor sex. Models are separated by bold black lines, and age is depicted by color where cubs are green, subadults are blue, and adults are brown. Points represent the odds ratio and error bars represent 95% confidence intervals around the odds ratio. Each point is compared to an unsupported actor reference group of the same age and sex class represented by the black dashed line.

patterns of intrinsic behavioral differences between the sexes were less clear, suggesting that these strong sex differences in the propensity to emit aggressive and submissive behaviors emerge primarily during adulthood. Our results support the earlier conclusion by Watts et al. (2009) and McCormick et al. (2021) that female spotted hyenas are the more aggressive sex, even after controlling for rank and subgroup size as factors influencing opportunities to act aggressively. Further, our analyses of unsolicited aggressive behavior also support prior work by Yoshida et al. (2016) on a much smaller dataset, where females were observed to be more aggressive toward members of the opposite sex than males, and where females were more aggressive toward males than males were to other males. Our result that adult males were more likely than adult females to submit without any observed provocation suggests another important intrinsic difference between the sexes, one that was also documented earlier by Smale et al. (1993). The fact that adult natal males were more submissive than adult females indicates that this pattern of adult male submissiveness is not driven purely by dispersal-induced changes in social support.

Our analysis of the outcomes of agonistic interactions revealed mixed support for both the social support and the intrinsic attributes hypothesis. Contrary to the predictions of the intrinsic attributes hypothesis, aggressing females were not more likely than aggressing natal males to receive submissive responses from their targets (**Figure 3A**). Instead, the only difference between the sexes over ontogeny was the reduced ability of adult immigrant males to elicit submission from adult females, which could be due to reduced social support available to immigrants. However, in support of the intrinsic attributes hypothesis, both adult immigrant males and adult natal males were more likely than adult females to submit to aggressors (**Figure 3B**). If this male-biased pattern of submission was driven exclusively by the actor's and recipient's potential for receiving social support, then immigrant males should have differed significantly from natal individuals of both sexes, because only immigrants had changed clans and lost their social support (Vullioud et al., 2019). However, as early as the first year of life, we observed that males were more likely than females to submit to aggressors, regardless of the sex of the aggressor (**Figure 3B**). These findings, particularly when considered in light of the striking sex differences in dominance within mixed-sex twin litters (Smale et al., 1995; Golla et al., 1999; Wahaj and Holekamp, 2006; Benhaiem et al., 2012), suggest that the behavioral tendencies associated with female dominance start to emerge well before male dispersal.

Our analysis of realized social support and its effect on the outcomes of aggressive interactions suggest that social support alone is insufficient to explain sex differences in dominance in this population of spotted hyenas. If social support was the basis of female dominance over males, we

expected to see that females would receive support at higher rates than males. Instead, adult females were considerably more likely than either adult immigrant males or adult natal males to act alone as aggressors (**Figure 4A**). A prior study found that females engage in coalitionary aggression more frequently than males (Smith et al., 2010), which might reflect that either females are more likely to receive support than males or females are more likely to engage in aggression than males. Our results clearly indicated that this pattern was driven by higher rates of aggression by females but a lower probability of receiving social support per aggressive act. The social support hypothesis also predicted that receiving support aids females in dominating males, but we found that adult females elicited submissive responses from adult immigrant and adult natal males when acting alone just as readily as when acting with support (**Figure 5**). Despite the lack of evidence for the social support hypothesis as the sole determinant of female dominance within this population of spotted hyenas, our results indicated that social support did shape agonistic interactions in some interesting ways. Realized social support improved the likelihood of adult females successfully dominating other adult females (**Supplementary Figure 3A**), supporting previous work which revealed that coalitionary aggression is an important mechanism producing rank change among female hyenas (Strauss and Holekamp, 2019). Most strikingly, although not part of our *a priori* predictions, we found an interesting pattern where hyenas of all age and sex classes were more likely to act alone when aggressing against males than females (**Figure 4B**). We interpreted this pattern as supporting both of the hypotheses under investigation: social support is most needed when acting against females, who are intrinsically more threatening adversaries.

Interestingly, realized social support slightly increased the likelihood that cubs and subadults would receive a submissive response during an agonistic encounter compared to cubs and subadults acting without support within our full models that included actor sex, recipient sex, and support (**Supplementary Figures 3B,C** and **Supplementary Table 7**). Some of this support may be mothers helping cubs win fights as part of the process of rank acquisition in the clan's dominance hierarchy (Engh et al., 2000; East et al., 2009; Strauss et al., 2020), particularly when subadult males are interacting with females (**Supplementary Figure 3C**). However, winning fights by female cubs was clearly also affected by the male recipient's tendency to concede defeat more readily than females when attacked (**Supplementary Figures 1A**, **3A**).

Altogether, our results point to social support and intrinsic sex differences as dual influences on dominance in this species. This contrasts with prior work, which reported that only the social support hypothesis explained sex differences in dominance in spotted hyenas (Vullioud et al., 2019), and multiple factors may explain this discrepancy. First, the two studies differed considerably in study design and methodology. For instance, we examined the behavior of adults, cubs, and subadults separately in this study (finding some interesting variation in dominance behavior across ontogeny), whereas prior work analyzed subadults and adults together. Most notably, Vullioud et al. (2019) included interactions between individuals from different social groups as well as within-group interactions, but we elected to focus only on within-group interactions because the factors influencing agonistic interaction outcomes within and between groups are often different (Majolo et al., 2020, [but see Vullioud et al., 2019]). Second, the two studies differed in the specific predictions tested: here, we tested predictions based on both potential for receiving social support and the realized social support individuals actually experience, whereas Vullioud et al. (2019) focused only on the potential for receiving social support. We made this choice because we felt that measuring realized social support was the most direct way of addressing its effect, but we agree with Vullioud et al. (2019) that the potential for receiving social support can influence interaction outcomes even if that social support is ultimately not delivered. A productive next step would be to investigate the relationship between potential and realized social support. If potential social support has as large an effect on interaction outcomes as realized social support, this may cause realized social support to appear to have a limited effect (e.g., **Figure 5**).

In addition to differences in study design, differences in the conclusions between the two studies might be due to population-level behavioral differences across the highly variable Serengeti–Mara ecosystem (Ginsberg et al., 1996). A productive avenue for further clarifying the basis of sex-biased dominance in this species would be to directly compare the behavior of natal males in these two populations to understand potential population-level differences. Additionally, given our findings that realized social support does aid adult immigrant males and subadult natal males in eliciting submission from female recipients, a further avenue of research would be to clarify exactly who, based on sex, rank, genetic relationships, and/or social networks, is supporting these males against females in a female-dominated society.

Finally, we conclude that multiple processes are likely to influence dominance in spotted hyenas, as also occurs in many other species (Lewis, 2020; Dehnen et al., 2022). We considered the phenomenon of female dominance in spotted hyenas in light of the general framework suggested by Lewis (2002) for assessing female power in animal societies. Lewis (2002) divides power into two categories, dominance and leverage, depending on the nature of the asymmetry between actor and recipient that generates power; in this framework, 'dominance' describes an asymmetry in physical capacities affecting the ability to use force. Female dominance is intrinsic among adult hyenas insofar as females are more

aggressive than males (**Figure 1**), and males are more submissive (**Figure 2**) and concede defeat much more readily than females (**Figure 3B**). However, dominance in this species is also based on social support, which helps cubs elicit submission from larger hyenas and helps adult females win fights against other adult females (Engh et al., 2000; Strauss and Holekamp, 2019). Thus, greater aggressiveness may be an intrinsic trait that enhances a female hyena's likelihood of winning fights with group mates, but the number of kin or other social allies available as potential supporters to a particular aggressor also affect its ability to win fights (Smith et al., 2010; Vullioud et al., 2019). We found that realized social support helped individuals of both sexes across age classes to dominate formidable females; in particular, realized social support helped immigrant males elicit submission from adult females, which they were very unlikely to achieve without support (**Supplementary Figure 3**). Overall, the results of our study add considerably to prior work demonstrating how support is crucial to rank acquisition (Holekamp and Smale, 1991; Engh et al., 2000; East et al., 2009), how it reinforces the established kin-structured dominance hierarchy among natal individuals (Smith et al., 2010; Holekamp et al., 2012; Vullioud et al., 2019), and how it influences competition among females (Strauss and Holekamp, 2019).

Data availability statement

The datasets generated during and/or analyzed during the course of this study are available in the Dryad repository: https://doi.org/10.5061/dryad.w6m905qsw.

Ethics statement

The animal study was reviewed and approved by Michigan State University Institutional Animal Care and Use Committee (IACUC Protocol 202200047, expiring 2/11/2025).

Author contributions

SM contributed to the conceptualization, methodology, curation of data, coding, analyses, visualization, writing of the manuscript, and supervision. ES, ZL, and TM contributed to the writing of the manuscript, methodology, analysis, and visualization. KH helped to conceptualize the project, contributed to data, funding, and other resources, and helped to draft the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.934659/full#supplementary-material

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Infanticide by Adult Females Causes Sexual Conflict in a Female-Dominated Social Mammal

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Infanticide by adult females includes any substantial contribution to the demise of young and inevitably imposes fitness costs on the victim's genetic fathers, thereby generating sexual conflict with them. Few if any studies have quantified the impact of infanticide by females on male reproductive success, the magnitude of sexual conflict this causes and possible counterstrategies males use against infanticidal females. We examine these topics in spotted hyena (*Crocuta crocuta*) clans, where females socially dominate breeding males and strong female mate-choice is independent of male social status. We consider two causes of infanticide by females, violent attacks on cubs and fatal maternal neglect. Violent attacks are predicted during periods of social instability at the top of the female linear dominance hierarchy and victims are expected to predominantly have mothers above median rank. Fatal maternal neglect, when starving litters are abandoned, is associated with monopolization of food in clan territories by high-ranking females, and victims are predicted to have mothers below median rank. Female perpetrators of violent attacks are expected to reduce the reproductive success of the fathers of their victims more than perpetrators of fatal maternal neglect. We tested these predictions using 30 + years of data (54 recorded violent attacks, 43 cases of fatal maternal neglect, DNA profiling of 1,671 individuals). Using long-term observations at communal dens we investigated whether males use counterstrategies against infanticide reported in other mammals. Due to female social dominance over breeding males, strong female mate-choice and prolonged offspring dependence on lactation in spotted hyenas, we predicted that these counterstrategies were unlikely to be used by males against females, thus no incidences of them were likely to be observed. Our results revealed that breeding males lost cubs to violent attacks at all stages of their reproductive tenure and to perpetrators with whom they did not sire offspring. Amongst known sources of paternity loss, violent attacks comprised 12.2% and maternal neglect 9.8% of cases. Violent attacks significantly reduced offspring production rates of breeding males, suggesting that infanticide by females generates sexual conflict. As predicted, no evidence of males using counterstrategies against infanticide by females were observed.

Keywords: infanticide, sexual conflict, resource competition, spotted hyena, DNA profiling, social instability

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INTRODUCTION

Infanticide in mammals is widespread and has been reported from rodents, bats, lagomorphs, cetaceans, pinnipeds, terrestrial carnivores and primates (Hoogland, 1985; Agrell et al., 1998; Blumstein, 2000; Digby, 2000; Knörnschild et al., 2011; Towers et al., 2018; Lowe et al., 2020; Brown et al., 2021). In adult mammals, intra-sexual reproductive competition is thought to favor the evolution of infanticide by providing perpetrators with the benefit of increased reproductive success (Hrdy, 1979; van Schaik, 2000; Lukas and Huchard, 2014, 2019; Palombit, 2015). Adult males are thought to use infanticide to gain additional mating partners, whereas infanticide by females is thought to increase access to resources required for successful reproduction (Digby, 2000; Stockley and Campbell, 2013; Lukas and Huchard, 2014, 2019; Walker et al., 2021). Perpetrators of infanticide exercise power over their victim and the victim's parents, and by killing offspring, perpetrators generate sexual conflict with the victim's parent of the opposite sex (Trivers, 1972; Arnqvist and Rowe, 2005). Parents of victims may evolve behavioral, reproductive or physiological counterstrategies to reduce their loss of reproductive success to infanticide (Palombit, 2015).

Perpetrators of infanticide may be either males or females, and in some species they may be individuals of both sexes, as in chimpanzees (*Pan troglodytes*) (Lowe et al., 2020; Walker et al., 2021) and killer whales (*Orcinus orca*) (Towers et al., 2018). Consideration of sexual conflict generated by infanticide has predominantly focused on the conflict between male perpetrators and the mothers of their victims (Palombit, 2015). Far less attention has been given to the sexual conflict generated by adult female perpetrators with the fathers of their victims whose reproductive success they undermine [see Lukas and Huchard (2019) for comparative analyses of the determinants of female infanticide]. In particular, to our knowledge, few studies based on free-ranging social mammals have attempted to quantify the fitness costs of losing paternity to infanticide by females. Similarly, discussion of counterstrategies against infanticide in mammals has mostly focused on female counterstrategies against infanticide by adult males and/or females (Hrdy, 1979; van Schaik and Kappeler, 1997; Digby, 2000) rather than male counterstrategies against infanticide by females. Our study aims to redress this imbalance by investigating the loss of reproductive success by breeding spotted hyena (*Crocuta crocuta*) males to infanticide by adult females within their clan, the level of sexual conflict infanticide by females generates and possible counterstrategies by males to limit paternity losses to infanticide.

In many social mammals, the reproductive success of females holding high social status is higher than that of subordinates (Pusey et al., 1997; Wasser et al., 2004; Stockley and Bro-Jørgensen, 2011; Wright et al., 2020). This is because socially dominant females have priority of access to resources necessary for reproduction (Clutton-Brock and Huchard, 2013) such as food or access to communal dens or burrows (Digby, 2000). This also applies to the spotted hyena (Holekamp et al., 1996; Hofer and East, 2003), a social carnivore which lives in multi-female, multi-male, fission-fusion groups called clans where all immigrant males are socially subordinate to natal females and their offspring (Kruuk, 1972; Frank, 1986).

Infanticide in Spotted Hyenas

Although both adult male and female spotted hyenas have been observed killing juveniles within their clan (Kruuk, 1972; Hofer and East, 1995; East et al., 2003; White, 2005; Brown et al., 2021), the incidence of infanticide by adult males (one observed case, plus one case of a male digging in a den, apparently intent on infanticide), was considered too low to be a male reproductive tactic (East et al., 2003). The findings of a recent study (Brown et al., 2021) and the results of this study indicate that the vast majority of infanticides in spotted hyenas are committed by adult females. Brown et al. (2021) reported that one in ten offspring in their study died of infanticide by adult females and that infanticide was most likely a response to competition over social status between matrilines. The effect of infanticide by females on the reproductive success of breeding males was not reported.

Infanticide results from actions by conspecifics that substantially contribute to the death of young of the same species (Hrdy, 1992). This has led to a focus on violent attacks by adults on juveniles, but conceptually need not be limited to such actions. For instance, one source of juvenile death in spotted hyenas is a form of infanticide termed facultative siblicide, when the dominant cub in a twin litter monopolizes access to maternal milk during nursing bouts, thereby starving its subordinate sib to death (Hofer and East, 1997, 2008; Golla et al., 1999; Benhaiem et al., 2012). Facultative siblicide will not be considered further, as we focus on two less studied causes of infanticide in spotted hyenas: (i) Violent attack, when aggression by an adult female results in the immediate death of a cub or substantial damage and death ensuing soon after. (ii) Fatal maternal neglect, when a mother fails to provide her offspring with sufficient milk to prevent its death from starvation, usually because long foraging excursions result in mothers not nursing their offspring for many days (Hofer et al., 2016). In such circumstances, females should suspend continued investment in current offspring if their own survival is at risk and investment in future offspring is likely to yield higher benefits (Williams, 1966; Trivers, 1972).

As spotted hyenas give birth throughout the year, infanticides may occur in any month of the year. Litters are small, normally one or two cubs, rarely three cubs, which in our study population all three cubs never survive, and maternal input into offspring is high, in terms of highly nutritious milk produced throughout a long lactation period of 12–20 months (Holekamp et al., 1996; Hofer and East, 2003; Hofer et al., 2016). By contrast, the contribution of fathers to provisioning offspring is negligible. In our study population, high-ranking females monopolized food resources within clan territories, resulting in low-ranking females using long-distance commuting trips (to distant locations containing abundant migratory ungulates) throughout most of the year, to fuel the high cost of lactation, whereas high-ranking females generally only commuted when prey density in the clan territory was at its lowest (Hofer and East, 1993c; Gicquel et al., 2022). Cubs remain at the communal den for at least their first 12 months of life, and when threatened by aggressive individuals

in the clan, they retreat into narrow and deep underground burrows where adults cannot reach them (Golla et al., 1999).

Male Social Status

All immigrant males are socially subordinate to adult females and their offspring in their clan (Frank, 1986). At immigration, males acquire the lowest social position in a clan, by taking the lowest rank in the male linear dominance hierarchy which functions as a stable social queue (East and Hofer, 2001). Males increase in social rank as more dominant males die or disperse elsewhere. Physical contests between immigrant males to increase their status are rare, thus high-ranking immigrant males are those with the longest tenure (East and Hofer, 2001). Although most breeding males in a clan are immigrants, occasionally males do not disperse and become breeding males in their natal clan, in which case they join the breeding male hierarchy ahead of the immigrant males (East and Hofer, 2001; Höner et al., 2007).

In our study population, all breeding males conduct long-distance foraging excursions when large aggregations of migratory herbivores are absent from their territory (Hofer and East, 1993a,b). High-ranking males have priority of access to food resources in the clan territory over low-ranking males (Frank, 1986) which may explain why high-ranking males are more often in our study clan territories than low-ranking males (East and Hofer, 1991), particularly at the communal den, which is an important social center of the clan (East et al., 2013). Low-ranking males are present at communal dens less often, typically remain at dens for shorter periods than high-ranking males, and rarely venture close to communal dens, unlike high-ranking males (East et al., 2013). This predicts that high-ranking males are more likely to witness violent attacks by females on cubs, and are better placed to use counterstrategies to protect their offspring against these violent attacks, than low-ranking males.

Female Mate-Choice and Male-Female Associations

The unusual anatomy of female reproductive organs (Matthews, 1939), in particular the penile clitoris positioned between the hind legs, ensures that copulation cannot be successful without the complete cooperation of females (East et al., 1993). Genetic studies on the paternity of offspring provide strong evidence that female mate-choice preferences do not necessarily match that of breeding males (Engh et al., 2002; East et al., 2003; Höner et al., 2007). For example, high-ranking males attempt to monopolize access to high-ranking females (East and Hofer, 2001; Szykman et al., 2001) but genetic paternity of cubs produced by high-ranking mothers is not skewed toward high-ranking males (Engh et al., 2002; East et al., 2003; Höner et al., 2007) and there is little evidence that coercion of females is an effective tactic to secure paternity (East et al., 2003). Thus female mate-choice is a likely source of sexual conflict in spotted hyenas (East et al., 2003).

Currently, little is known about the male traits that females prefer, beyond those associated with avoidance of inbreeding with close male relatives in the clan (Höner et al., 2007). This chiefly entails young females, regardless of their social status, selecting males that joined the clan after the females was born, to sire their cubs.

Breeding males foster associations with females in their clan (Szykman et al., 2001). Female mate-choice to avoid inbreeding is apparent in male-female associations in that older adult females are more tolerant of approaches by longer-tenured than shorter-tenured males, and younger adult females are more tolerant of approaches by shorter-tenured than longer-tenured males (East and Hofer, 2001). Throughout their lives, female produce offspring sired by several males and there is evidence that females mate with multiple males to promote sperm competition and confuse paternity (East et al., 2003).

Paternity Losses to Infanticide by Adult Females

Using direct observations of infanticide during observation sessions primarily at clan communal dens, from an ongoing long-term study in the Serengeti National Park initiated in 1987, coupled with microsatellite DNA profiling of 1,671 individually known spotted hyenas (adult males, adult females and offspring), we determined the genetic sires of cubs that died from infanticide by adult females, the level of sexual conflict the actions of these females generated with the victims' fathers and potential male counterstrategies.

We predicted that the cost of infanticide to individual breeding males, in terms of reduced reproductive success, would depend on the type of infanticide (violent attack by females or fatal maternal neglect) and the social status of mothers, and we explored whether it varied with female age. High-ranking females have a higher reproductive success than low-ranking females because they give birth to their first litter at an earlier age, and their cubs have higher growth rates and chances of survival to adulthood than those of low-ranking females (Holekamp et al., 1996; Hofer and East, 2003; Ferreira et al., 2019). Thus siring cubs with high-ranking females provides breeding males with fitness benefits. As violent infanticide by adult females is considered an expression of female-female competition for resources essential for reproduction (Lukas and Huchard, 2019) and resource competition within our clan territories is most intense among high-ranking females (Hofer and East, 1993c; Goymann et al., 2001), we predicted that offspring sired with high-ranking mothers should be particularly vulnerable to fatal violent attacks by high-ranking females, and infanticide by violent attacks should increase during periods of social unrest between competing coalitions of high-ranking females.

As food resources within the clan territory are monopolized by high-ranking females, low-ranking females fuel the high energetic cost of lactation (Hofer et al., 2016) by regularly commuting long distances between their offspring at the clan communal den and distant aggregations of migratory ungulates throughout many months of the year (Hofer and East, 1993c; Gicquel et al., 2022). As a result of these long-distance commuting trips, cubs of low-ranking mothers have longer (in terms of days) intervals between nursing bouts and a lower intake of milk than high-ranking cubs (Hofer et al., 2016). Regular long-distance commuting trips increase fecal glucocorticoid levels in adult

females (Goymann et al., 2001) and are associated with elevated infection loads of costly gastrointestinal parasites in lactating, low-ranking females, which may be indicative of down regulation of immune processes (East et al., 2015). At communal dens, harassment by high-ranking females disrupts attempts by low-ranking females to nurse their offspring and can prevent low-ranking females from attempting to nurse their offspring (Golla et al., 1999). For these reasons we predicted that males that sire offspring with low-ranking mothers are particularly vulnerable to infanticide by maternal neglect.

As infanticide by violent attack has been estimated to be a relatively important source of cub mortality (Brown et al., 2021), we predicted that infanticide by violent attacks should reduce male reproductive success more than by maternal neglect. Thus the magnitude of sexual conflict between female perpetrators and the genetic fathers of their victims would be higher for infanticide by violent attacks than fatal maternal neglect.

Potential Male Counterstrategies Against Infanticide of Their Offspring by Adult Females

Various possible counterstrategies against violent infanticide have been reported in social mammals. These include counter attacks by the victim's parent(s), and the formation of alliances with individuals in a group (Packer and Pusey, 1983; Agrell et al., 1998; Fruteau et al., 2010; Palombit, 2015), as well as dispersal, typically by adult females (Pusey and Packer, 1994; Sterck and Korstjens, 2000; Zhao et al., 2011). Infanticide by maternal neglect in species with biparental provisioning of offspring might be prevented by increased paternal provisioning of food to compensate undernourished offspring. More generally, bet-hedging in which males sire cubs with many females so that paternity lost due to infanticide incurred by one female partner is compensated by the survival to adulthood of offspring sired with other partners, might be a potential counterstrategy against various causes of infanticide. It is also conceivable that males could prefer or avoid specific females with whom to sire offspring if this helped to minimize paternity losses from infanticide. Social dominance of females over breeding males, strong female mate-choice, and prolonged offspring dependence on lactation in spotted hyenas predict that breeding males are unlikely to use any of these counterstrategies against infanticide of their offspring by adult females.

METHODS AND STUDY SYSTEM

Study Population and Standard Methods

Infanticides were observed in five clans (Isiaka, Pool, Mamba, Songore, Campsite) located in the center of the Serengeti National Park (Serengeti NP) in Tanzania during observations periods primarily at the communal dens (Hofer and East, 1993a). Den observation periods at dawn and dusk lasted for 2 h or more. Incidences of infanticide, DNA profiling data and data used in the analysis of the effect of infanticides on the reproductive success of breeding males were obtained from the three main study clans (East et al., 2003) regularly monitored between 1987 and 2020 (Isiaka: May 1987–March 2020; Pool: November 1989–March 2020, Mamba: August 1999–March 2020). Dens in the Songore and Campsite clans were monitored less intensively between 1988 and 1995.

Individuals were identified by unique spot patterns, markings, and features using well established methods (Frank, 1986; Frank et al., 1990; Hofer and East, 1993a). The main study clans were well habituated to the presence of observers in vehicles, which permitted us to record detailed behavioral and life-history data at the clan communal dens and elsewhere. Females remained in their natal clan throughout their life, thus clans had several overlapping female generations (matrilineal society). Most males dispersed after they reached adulthood and immigrated into another clan. Some males became reproductively active in their natal group (East and Hofer, 2001). The term breeding male includes reproductively active natal males and immigrant males in a clan. Breeding tenure for natal males started on the date they first displayed behaviors of a reproductively active male. For immigrant males, breeding tenure started on the date they were first seen in a study clan (East and Hofer, 2001; Höner et al., 2007).

Females give birth to one or two cubs, very rarely three (Hofer and East, 2008) throughout the year (Hofer and East, 1995; Holekamp et al., 1996) after a gestation period of 110 days (Matthews, 1939). Their energetic and time investment per litter is amongst the highest in the order Carnivora, with cubs being completely dependent on maternal milk for the first 6 months and weaned at the age of between 12 and 20 months (Holekamp et al., 1996; Hofer et al., 2016). Cubs remain at the clan communal den until approximately 12 months old where they shelter in underground burrows that are too narrow for adults to access (Hofer and East, 1993c; Golla et al., 1999). Cubs were animals $<$ 12 months old, subadults were those between 12 and $<$ 24 months old and adults were those that were 24 months or older (Hofer and East, 2003; Hofer et al., 2016). We refer to offspring when we do not refer to specific age categories of individuals below 24 months.

Birth dates were either known or derived using several developmental characteristics of pelage, locomotion and aspects of physical appearance (Golla et al., 1999; East et al., 2003). The conception date of cubs was calculated by subtracting 110 days from their birth date. Cubs less than approximately 10 weeks old rarely emerged from the clan den during their mother's absence, but they can be located in an underground burrow close enough to the den entrance to permit infanticidal females to grab them. Adult spotted hyenas cannot enter the narrow underground chambers of a clan den, thus cubs that remain deep underground cannot be grabbed by infanticidal females.

For each clan, the linear dominance hierarchies for adult females and breeding males were constructed from submissive behaviors recorded *ad libitum* during dyadic interactions between adults of the same sex (see East and Hofer, 2001; East et al., 2003). Dominance hierarchies were adjusted after each loss or recruitment of an adult and when dyadic interaction data revealed that an individual had increased or fallen in rank. To facilitate the comparison of ranks across clans of different sizes we

computed standardized ranks. This measure placed the rank of an individual evenly between the highest (standardized rank + 1) and lowest (standardized rank −1) rank (Goymann et al., 2001; East et al., 2003). Low-ranking individuals in both the adult female and breeding male dominance hierarchies were termed low-ranking when they held a standardized rank between −1 and 0, and high-ranking when they held a rank above 0.

Female social status determined access to food within a clan's territory and the proportion of the year during which females undertook regular long-distance foraging trips outside the clan territory to forage in areas containing large aggregations of migratory herbivores (Hofer and East, 1993b, 2003). In brief, when a clan territory only contained resident herbivores, prey abundance was low (∼7.2 animals/km^2) and adult females, regardless of social status, predominantly foraged elsewhere. When resident herbivores plus low numbers of migratory herbivores were present in the clan territory, prey abundance (∼31.0 animals/km^2) was sufficient to support females in the upper third of the female dominance hierarchy, whereas lower-ranking females needed to forage elsewhere. When territories contained large numbers of migratory herbivores (∼238.5 animals/km^2) all adult females foraged within their clan territory, mothers nursed their cubs daily, and thus maternal den attendance was high (Hofer and East, 1993b,c). Milk-dependent offspring remained at the clan communal den when their mother was foraging (Hofer et al., 2016). Long-distance commuting trips outside the clan territory resulted in maternal absences from their offspring of between usually 2–9 days, a substantial decrease in maternal den attendance (Hofer and East, 1993c). As a result, lower-ranking mothers spent a larger proportion of the year commuting and therefore transferred much less milk to their cubs than higher-ranking females (Hofer and East, 2003; Hofer et al., 2016; Gicquel et al., 2022).

Infanticide by Violent Attacks

We categorized the level of certainty we placed on records of violent attacks as follows: (i) "Observed" infanticides: Aggression causing the death, or in two cases substantial damage (with death following subsequently) of cubs, witnessed by a member of the project. As reported by Brown et al. (2021), violent attacks typically involved a bite to the head of a young cub. (ii) "Likely" infanticides: Presence of a recently dead cub (or part of a cub's carcass) which had shown no recent clinical signs of disease, no signs of starvation and there was no evidence that death had resulted from other possible causes (e.g., wounds consistent with predation by large cats or being hit by a vehicle). If a cub carcass was carried or consumed by a clan member, this individual was not necessarily assumed to have committed infanticide. In some of these cases, females were observed with a recently killed carcass of a cub, and these females were the only individuals present with blood on their mouths. (iii) "Suspected" infanticides: The sudden disappearance of an apparently healthy and well-nourished cub during a period of social instability (see below) among high-ranking females.

Infanticide by Fatal Maternal Neglect

We defined fatal maternal neglect as cases of cubs that were visibly extremely undernourished prior to their disappearance, with subsequent confirmation that the mother had survived, so litter death was not caused by the death of the mother. It takes on average 3 weeks for cubs devoid of any nutrition to starve to death following the disappearance of their mother (Hofer and East, unpublished data). Cubs markedly changed in their behavior during the last few days prior to death, when they became listless and lethargic, and frequently called for their mother (whoop, East and Hofer, 1991). Litters recorded as dying of fatal maternal neglect did not show clinical signs associated with pathogen infection such as labored breathing, discharge from eyes or nose, neurological disorders and lack of response to social stimulation (East et al., 2008; Marescot et al., 2018). Undernourished members of a twin litter were only classified as having died from maternal neglect if the high intensity of sibling aggression and the substantial difference in body size associated with facultative siblicide was not observed (Hofer and East, 1997, 2008). Cases of facultative siblicide (Golla et al., 1999; Hofer and East, 2008) were not included in either category of infanticide and are not considered further in this study. It is possible that the cubs we classified as dying from maternal neglect could have disappeared because of an unobserved violent attack by other females, in which case our records of neglect are a maximum estimates for fatal maternal neglect.

Our definition of fatal maternal neglect is a functional definition in that it solely focuses on the question whether the mother substantially contributed to the death of the cub because the mother did not nurse its offspring sufficiently frequently to prevent death by starvation. Maternal den attendance is an index of the frequency at which cubs receive milk (Hofer et al., 2016). To indicate the low rate of den attendance by females whose cubs died of neglect, we compared maternal den attendance in the 4 weeks prior to offspring death for cubs which died from fatal maternal neglect with that for cubs which died from violent attacks. The median proportion of observation periods when mothers of neglected cubs were at the den was 13.2% [mean 17.5%, 95% confidence limits (CL) 12.0%–23.0%, n = 38, with a median of 25.5 observation periods in these 4 weeks], or approximately 1 in 8 observation periods, equivalent to one visit to the communal den per 4 days. For mothers of victims of violent attacks the median proportion of observation periods when mothers were at the den was 24.0% [mean 26.3%, 95% CL 20.5%–32.1%, n = 49, with a median of 22 observation periods in these 4 weeks], approximately 1 in 4 observation periods or a visit to the communal den every 2 days, a significant difference (Mann–Whitney U-test, U = 673, $n_{neglect}$ = 38, $n_{violent}$ = 49, p = 0.027).

Periods of Social Instability

In all three main study clans, coalitions of females regularly challenged the reigning alpha female and her coalition partners, typically daughters, and when successful, took over the top ranks ("coups"). During such periods of social unrest, serious fights

were observed between participating females, much more intense than during normal dominance interactions, causing injuries (some severe) to the head, neck, shoulders and feet of participants (**Figure 1**). We termed these "periods of social instability," and the remaining time "periods of social stability." There were a total of 58 periods of social instability with coups or attempted coups. These periods occurred regularly, although not frequently, in all three study clans. Although these periods involved a decisive and typically short period of aggressive fighting between two opposing coalitions when the outcome of the challenge is decided, the build-up and the after-effects are not necessarily limited to that particular day but may take longer, as females return from commuting trips to a new social order. We therefore defined narrow and broad time periods of social instability as ± 2 days and ± 30 days around the date of decision. If a second coup or coup attempt followed soon after a previous coup and fell within the definition of broad time periods around the previous coup event, then both coups were amalgamated to a single period of instability. This amalgamation is responsible for smaller sample sizes for the broad definition periods. In order to test the prediction that periods of social instability and the associated increase in aggression elevate the likelihood of infanticide, we compiled annual mortality rates of offspring for both narrow and broad definitions of periods of social instability and the intervening periods of stability.

DNA Profiling

Genetic samples (gut epithelial layer from feces, feces or tissue) were obtained from hyenas and genotyped using up to nine microsatellite loci for microsatellite DNA profiling as previously described (East et al., 2003, 2009; Wilhelm et al., 2003; Höner et al., 2007). Maternity and paternity were determined using maximum likelihood methods as implemented in CERVUS (Marshall et al., 1998; Kalinowski et al., 2007). Adopted cubs were therefore correctly allocated, in terms of mate-choice to their genetic mother. Candidate fathers included reproductively active natal males and immigrant males throughout the duration of their breeding tenure in a clan plus a 90 day period before and after the start and end of their tenure. Maternity and paternity were accepted if they exceeded the threshold for a 95% assignment. This resulted in the successful assignment of fathers (in addition to mothers) for 1,245 cubs. The mean expected heterozygosity was 0.8514, mean polymorphic information content (PIC) was 0.8346, combined non-exclusion probability for a parental pair was 4.119×10^{-9}, mean proportion of alleles typed was 0.9775 and the error rate, set at 1%, was 0.008.

FIGURE 1 | Damaging physical contests between competing high-ranking female coalitions during a period of social instability (coup). Photo: MLE and HH.

Statistical Analyses

We used non-parametric tests, in some cases with exact *P* values approximated by 10,000 Monte Carlo simulations, following the procedures recommended by Conover (1999) and Hollander et al. (2014). We applied the Mann–Whitney *U*-test to compare two independent groups. For the comparison of annual mortality rates we used the permutation test with general scores for paired samples, as this is the most powerful test for paired samples, to investigate differences between adjacent (paired) periods of social stability preceding periods of social instability.

Records of the tenures of immigrant males were complete provided they were observed to enter the study clan and had completed their tenure by either dying or dispersing to another clan before the end of the study period. The tenure of natal breeding males started on the date they were first observed exhibiting behaviors typical of immigrant males toward females in their clan and their tenures were complete when they died or dispersed to another clan. Some males were already members of the clan at the beginning of the study, or were members of the study clans and still alive at the end of the study. Their recorded tenures are therefore minimum estimates and constitute right-censored data (Kalbfleisch and Prentice, 1980). Males present at the beginning of the study were excluded from those comparisons when the exact length of tenure on the conception date of a victim was required in an analysis. In order to compare tenures between groups of males, we conducted a survival analysis and calculated non-parametric survivorship functions as Kaplan–Meier estimates, which incorporated right-censored data. We compared the tenures of males who lost cubs from violent attacks with males who did not with the non-parametric generalized Wilcoxon test known as Breslow–Gehan (or Gehan–Breslow) test.

Estimates are given as means with their 95% confidence limits (CL) unless otherwise stated, and probabilities are for two-tailed tests. Statistical analyses were performed with SYSTAT 13.0 (Systat Inc., San Jose, CA, United States) and StatXact 11.0 (Cytel Inc., Cambridge, MA, United States). **Figures 2**, **3** were plotted in R 4.1.2 (R Core Team., 2021) using the packages *ggplot2* version 3.3.5 (Wickham, 2016) and *ggprism* version 1.0.3 (Dawson, 2021).

RESULTS

Infanticide by Adult Females in the Main Study Clans

Of the 1,346 offspring which died in the Isiaka, Mamba and Pool clans before reaching adulthood (at the age of 24 months), 54

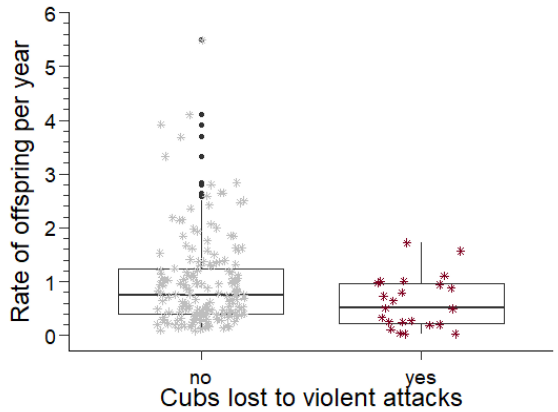

FIGURE 2 | Rates of offspring produced per year by males who did and did not lose cubs to violent attack, adjusted for losses of cubs to the estimated rate of violent attack. The box comprises the interquartile range, the horizontal line is the median, the whiskers cover the range of values 1.5 times the value of the interquartile range, the asterisks indicate data points in the range between 1.5 and 3 times the value of the interquartile range, and open circles values beyond 3 times the value of the interquartile range.

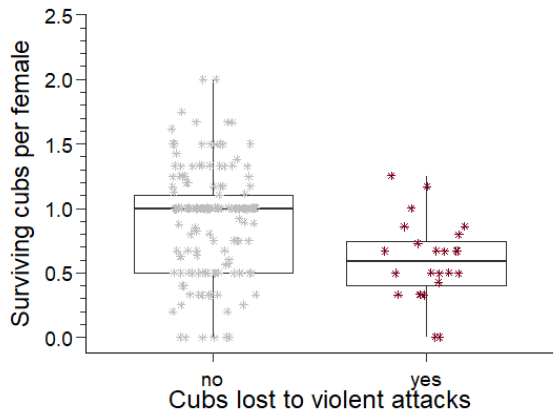

FIGURE 3 | The number of cubs produced per mother by males who lost cubs to violent attack and those who did not. The box comprises the interquartile range, the horizontal line is the median, the whiskers cover the range of values 1.5 times the value of the interquartile range.

died from violent attacks, 43 died from neglect by their surviving mothers, 345 died from other known sources of mortality (e.g., disease, predation, traffic accidents), and 904 died of unknown causes. The overall incidence of violent attacks and fatal maternal neglect in all offspring, including deaths from unknown causes, was therefore 4.0% and 3.2%, respectively. Within the 442 offspring with known sources of mortality, the incidence of violent attacks was 12.2%, and for death from fatal maternal neglect it was 9.8%.

As predicted, annual rates of overall offspring mortality were substantially, and significantly, higher during periods of social instability than during periods of social stability (**Table 1**). These increases were mostly driven by cases of violent attacks, as demonstrated by their high incidence amongst known sources of mortality (**Table 1**), for both narrow and broad definitions of periods of instability.

The mean age of the 54 cubs in the main study clans when killed by violent attacks by females was 115.6 days (95% CL 90.3–140.9 days). Most cubs were killed by violent attacks during periods when prey abundance was low (n = 25 cases) or medium (n = 25 cases), few violent attacks occurred when prey was abundant (n = 4 cases). There were 43 cases of fatal maternal neglect in the three main study clans. The mean age of cubs when killed by maternal neglect was 151.5 days (95% CL 116.2–186.8 days). Most cubs killed by fatal maternal neglect occurred in periods when prey abundance was low (n = 21 cases) or medium (n = 16 cases), few cubs were killed by maternal neglect when prey was abundant (n = 3 cases).

Overall Incidence of Violent Attacks

In total, 56 violent attacks were recorded in five clans, including the main study clans (Isiaka, Mamba, Pools), and one attack each in the Songore and Campsite clans (Hofer and East, 1993a). These included: (i) 24 "observed" cases when an adult female in a clan was witnessed (by a member of the project) to lethally damage the cub of another female member of the clan. In 23 cases this involved crushing bites to the head, including one case when a mother grabbed her cub when she was aggressively harassed by a coalition of females, and the mother (probably accidentally) crushed its skull. (ii) 20 "likely" cases when a cub's death was judged to be caused by a violent attack by a conspecific because of the occurrence of a crushed skull and the absence of the deep canine puncture wounds typical of predation by lions (*Panthera leo*) or leopards (*Panthera pardus*). (iii) 12 "suspected" cases of healthy cubs of high-ranking females that disappeared unexpectedly either during or shortly after (within 2 days) of a coup or a failed coup that involved intense aggression between competing female coalitions. For the 32 cases, for which we knew (24) or suspected (8) the identity of the killer, the perpetrators were adult females of the same clan in 30 cases. One case involved an immigrant male killing a starving, moribund cub, and one case was a subadult male offspring (of a high-ranking mother) which killed and consumed an offspring of a lower-ranking female.

Paternity Losses to Violent Attacks and Fatal Maternal Neglect

Does infanticide by females reduce offspring production rates of breeding males and thereby generate sexual conflict? During the study period, there were 372 breeding males (immigrants and reproductively active natal males) in the three study clans, of which 281 males (75.5%) were genetically profiled, and 197 (70.1%) sired at least one cub. On average these 197 males sired a mean of 6.3 cubs (95% CL 5.5–7.2) during a mean tenure of 7.7 years (95% CL 6.8–7.8), and on average 3.7 of their offspring survived to adulthood (95% CL 3.2–4.3).

Considering the 197 males with at least one genetically typed cub, these males lost on average 0.16 offspring to violent attacks (95% CL 0.09–0.23) and 0.08 to maternal neglect (95% CL 0.03–0.13). These data originate from 31 of the recorded 54 cubs experiencing violent attacks, and 15 of the 43 cases of

TABLE 1 | Number of deaths, incidences and rates of annual mortality for all spotted hyena offspring (Total) which died before reaching adulthood, as well as for those experiencing violent attacks (Violent) and infanticide by fatal maternal neglect (Neglect), during periods of social instability (coups) and stability in the three main study clans.

Source	All cub deaths	%	Known cub deaths	%	Mean mortality rate [year^{-1}] and 95% conf. limits	*n*	All cub deaths	%	Known cub deaths	%	Mean mortality rate [year^{-1}] and 95% conf. limits	*n*	Permutation test with general scores for paired samples
	Periods of social instability, narrow definition: coup ± 2 days						**Periods of social stability**						
Total	42	100.0%	17	100.0%	54.3 [26.6, 82.0]	55	1304	100.0%	425	100.0%	12.9 [11.0, 14.7]	58	$z = 2.815$, $p = 0.0049$
Violent	12	28.6%	12	70.6%	15.2 [4.9, 25.5]	55	42	3.2%	42	9.9%	0.5 [0.2, 0.8]	58	$z = 2.684$, $p = 0.0073$
Neglect	2	4.8%	2	11.8%	2.7 [−2.7, 8.0]	55	41	3.1%	41	9.6%	0.3 [0.1, 0.6]	58	$z = 0.867$, $p = 0.386$
Others	3	7.1%	3	17.6%			342	26.2%	342	80.5%			
Unknown	25	59.5%					879	67.4%					
	Periods of social instability, broad definition: coup ± 30 days						**Periods of social stability**						
Total	173	100.0%	46	100.0%	20.3 [15.9, 24.8]	49	1173	100.0%	396	100.0%	12.0 [10.0, 14.1]	52	$z = 3.273$, $p = 0.0017$
Violent	18	10.4%	18	39.1%	2.1 [0.9, 3.2]	49	36	3.1%	36	9.1%	0.4 [0.1, 0.6]	52	$z = 2.817$, $p = 0.0048$
Neglect	6	3.5%	6	13.0%	0.6 [−0.5, 1.7]	49	37	3.2%	37	9.3%	0.3 [0.1, 0.6]	52	$z = 0.574$, $p = 0.566$
Others	22	12.7%	22	47.8%			323	27.5%	323	81.6%			
Unknown	127	73.4%					777	66.2%					

n, number of periods of social stability or social instability.

fatal maternal neglect for which we obtained genetic samples and identified the father with 95% confidence. As we did not establish the genetic fathers of all cubs lost to violent attacks and maternal neglect, our calculated losses are minimum estimates that underestimate the true losses. An estimate of the true loss ("adjusted") for the situation when the identities of all fathers would be known for the cubs experiencing violent attacks or maternal neglect is the recorded loss multiplied by the total number of cases divided by the genetically typed cases. For cubs lost to violent attacks this is 0.16 × 54/31, equal to 0.28 cubs lost to violent attacks, and for cubs lost to maternal neglect this is 0.08 × 43/15, equal to 0.23 cubs lost to maternal neglect.

As predicted, violent attacks reduced male reproductive success more than fatal maternal neglect. The recorded losses of offspring are equivalent to an average of 3.3% (95% CL 1.6%–4.9%) of offspring deaths to violent attacks and 1.2% (95% CL 0.4%–2.0%) to maternal neglect. Adjusted for the incomplete identification of fathers of offspring that died from violent attacks and maternal neglect, these losses for each male on average amount to 5.7% (95% CL 2.9%–8.5%) of offspring deaths from violent attacks, to 3.5% (95% CL 1.2%–5.9%) to fatal maternal neglect and the combined value for violent attacks and fatal maternal neglect to 9.2% (95% CL 5.6–12.8%).

The annual rates at which breeding males sired offspring, their sired offspring reached adulthood, the rates at which their offspring were killed by violent attacks or died from fatal maternal neglect, and the rate of loss when both causes of paternity loss were combined are summarized in **Table 2**. If losses caused by violent attacks or fatal maternal neglect were sufficiently high to affect the rate of offspring production by males, then males with and without such losses should differ in the annual rate of offspring production after the losses had been subtracted from the overall rate of production. We therefore removed the adjusted (see above) rates of losses from the total rate of offspring production and then compared annual rates of offspring production between males with and without losses to violent attack or fatal maternal neglect. These offspring production rates (**Table 2**) were significantly lower (**Figure 2**) in males with losses from violent attacks than in males without (Mann–Whitney *U* test, $U = 2{,}717$, $n_{infanticide} = 24$, $n_{noinfanticide} = 173$, $p = 0.014$, **Table 2**), and also lower in males with losses from fatal maternal neglect than in males without ($U = 1{,}600$, $n_{infanticide} = 11$, $n_{noinfanticide} = 186$, $p = 0.002$, **Table 2**).

Considering all males for which we have complete reproductive tenures ($n = 265$), 135 males produced at least one offspring. For these males, we collated the total number of offspring they sired, the number of different females they sired offspring with, and the total number of offspring that survived to adulthood. The ratio of the number of offspring that survived to adulthood divided by the number of females each male sired offspring with is an indicator of the reproductive success of each male per female partner. For males with losses to violent attacks this reproductive success was approximately half of the reproductive success for males who did not suffer such losses ($U = 2{,}871$, $n_{infanticide} = 24$, $n_{noinfanticide} = 173$, $p = 0.002$, **Figure 3**).

We predicted that the fitness cost of infanticide by females to fathers depended on the social status of the mothers of victims. To assess whether offspring of high-ranking females were particularly vulnerable to violent attacks, we compared the mean standardized ranks and age of mothers of cubs killed in violent attacks with those lost to maternal neglect. On the day of conception for cubs killed in violent attacks, the mean standardized rank of their mothers was + 0.25 (95% CL 0.08–0.42), and for cubs lost to maternal neglect, it was −0.17 (95% CL −0.30 to −0.04). These standardized ranks differed significantly (Mann–Whitney *U*-test, $U = 1581.5$, $n_{violent} = 54$, $n_{neglect} = 43$, $p = 0.001$).

On the day of conception of cubs lost to violent attacks, mean maternal age was 6.63 years (95% CL 5.72–7.53 years), and for cub lost to neglect, mean maternal age was 7.13 years (95% CL 6.10–8.18 years). These ages did not differ ($U = 728.5$, $n_{violent} = 48$, $n_{neglect} = 35$, $p = 0.30$).

Potential Counterstrategies by Breeding Males

For secondary dispersal to be a potential counterstrategy by males, the chance of paternity loss to infanticide would need to increase with male tenure, as the longer a male stays in a clan, the chance that infanticide will kill one of his offspring is expected to increase. This was indeed the case for males who had lost cubs to violent attacks by females. Their mean tenure was 10.7 years (survival analysis, Kaplan–Meier estimate, $n = 24$, 95% CL 9.1–12.2 years), significantly higher than the mean tenure of 8.3 years of males who had not ($n = 173$, 95% CL 7.6–9.1 years, Breslow-Gehan test, $\chi^2 = 5.66$, $df = 1$, $p = 0.017$). For males who had lost cubs to fatal maternal neglect, mean tenure was 11.0 years (survival analysis, Kaplan–Meier estimate, $n = 11$, 95% CL 8.6–13.4 years), which tended to be higher than the mean tenure of 8.4 years of males who had not ($n = 186$, 95% CL 7.7–9.1 years, Breslow-Gehan test, $\chi^2 = 2.08$, $df = 1$, $p = 0.15$). However, breeding males lost offspring they had sired to infanticide (violent attack and fatal maternal neglect) by adult females regardless of the duration of breeding tenure and dominance status on the date of conception (**Figure 4**). Violent attacks affected 24 of the 197 males (12.2%), fatal maternal neglect affected 11 (5.6%) of these males. There were 32 males affected by either of these causes of lost paternity (16.2%) and three by both (1.5%). Amongst these 197 males, total tenure was complete for 135 individuals (mean 6.9 years, 95% CL 6.2–7.5 years), for 62 males, their tenure was ongoing at the beginning or the end of the study, with a mean of 8.3 years (95% CL 7.5–9.1 years). There was no difference in the incidence of infanticide amongst males whose tenure was complete (11.9%) and those with an ongoing tenure (12.9%, likelihood ratio test, $G = 0.044$, $n_{on\text{-}going} = 65$, $n_{complete} = 135$, $p = 0.835$). Total tenures of males that lost cubs to either violent attacks or fatal maternal neglect were approximately 2.5 years longer than tenures of males who had not.

Do males attempt to reduce their chance of losing offspring to infanticide through siring cubs with a particularly large or small number of different females (bet-hedging)? Males who lost cubs to violent attacks sired offspring with a similar number

TABLE 2 | Annual rates of offspring produced or lost by breeding males.

Parameter	Mean	95% CL	*N*	Mean	95% CL	*n*
	Overall rates					
Offspring year^{-1}	0.97	0.85, 1.08	197			
Offspring that reached adulthood year^{-1}	0.56	0.48, 0.64	197			
Offspring lost to violent attacks year^{-1}	0.02	0.01, 0.03	197			
Offspring lost to maternal neglect year^{-1}	0.008	0.003, 0.014	197			
Offspring lost to violent attacks and maternal neglect year^{-1}	0.03	0.017, 0.042	197			
Offspring production rates for which losses were adjusted for underestimating identity of fathers in cases of violent attacks or neglect, split by males losing or not losing offspring to violent attacks and/or neglect						
	Males without losses to infanticide			**Males with losses to violent attacks and/or neglect**		
Offspring year^{-1}, adjusted for losses from violent attacks	0.98	0.85, 1.11	173	0.57	0.36, 0.79	24
Offspring year^{-1}, adjusted for losses from maternal neglect	0.98	0.86, 1.11	186	0.32	0.12, 0.53	11
Offspring year^{-1}, adjusted for losses to violent attacks and/or maternal neglect	1.00	0.86, 1.13	165	0.45	0.28, 0.62	32

CL, confidence limits.

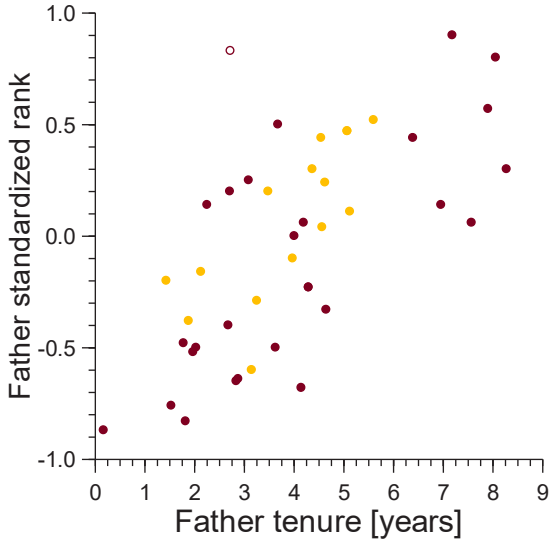

FIGURE 4 | Male standardized rank in relation to breeding tenure for males that lost cubs to violent attacks (burgundy) and maternal neglect (amber) on the day of the conception of the victim. Filled symbol: immigrant males, open symbol: natal male.

of different females (mean number 0.64 year^{-1}, 95% CL 0.49–0.78 year^{-1}) as those males who did not lose cubs to violent attacks (mean number 0.69 year^{-1}, 95% CL 0.60–0.79 year^{-1}, U = 1,928, $n_{infanticide}$ = 24, $n_{noinfanticide}$ = 173, p = 0.57). Similarly, males who lost cubs to fatal maternal neglect sired offspring with a similar number of different females (mean number 0.55 year^{-1}, 95% CL 0.44 –0.66 year^{-1}) as those who did not (mean number 0.69 year^{-1}, 95% CL 0.60–0.78 year^{-1}, U = 1,011, $n_{neglect}$ = 11, $n_{noneglect}$ = 186, p = 0.95). These results suggest that a male's chance of losing paternity to violent attacks or fatal maternal neglect is not affected by the number of different females it sired offspring with.

Female Mate-Choice and the Magnitude of Sexual Conflict

We predicted that the genetic parents of the victims of infanticide should conform to expected female mate-choice patterns to avoid inbreeding, as we expected mothers of infanticide victims to have selected males that immigrated into their clan after they were born. Most females (78.4%, n = 37) applied this mate choice rule (**Figure 5**, points to the right of the line), and this was the case for both mothers that lost a cub to violent attack (79.2%, n = 24) and fatal maternal neglect (78.6%, n = 11, **Figure 5**). The tenure of fathers on the conception date of their cub which died from fatal maternal neglect grew with maternal age at the conception date of the victim (ρ = 0.615, n = 13, $p < 0.05$, **Figure 5**) as expected from female mate-choice based on male tenure.

The tenure of fathers on the conception date of their cub which died from a violent attack was unrelated to the age of the female perpetrator of the violent attack (Spearman's correlation coefficient, ρ = 0.066, n = 15, **Figure 6**), thus adult female perpetrators, regardless of age, generated sexual conflict with breeding males.

There was no relationship between the standardized rank of the genetic mother in the female dominance hierarchy and that of the genetic father in the breeding male dominance hierarchy on the date of conception for cubs lost to violent attacks (ρ = 0.14, n = 31, *NS*, **Figure 7**), and those lost to fatal maternal neglect (ρ = −0.19, n = 15, *NS*, **Figure 7**). This indicates that sexual conflict generated by infanticide by adult females is not higher for breeding males above median rank, as would be expected in species where paternity of offspring in a social group is skewed toward dominant male(s).

Finally, we asked whether victims of infanticide by violent attacks and the dependent offspring of the perpetrator shared

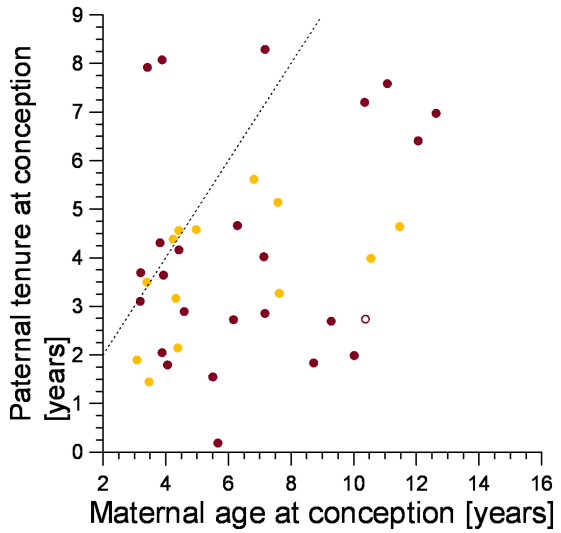

FIGURE 5 | The tenure of fathers in relation to the age of mothers on the date they conceived an offspring that was later a victim of either infanticide by violent attack (burgundy) or maternal neglect (amber). Filled symbol: immigrant males, open symbol: natal male. Points to the right of the broken line represent males which immigrated into the clan after the female was born, those to the left of the broken line immigrated before the female was born.

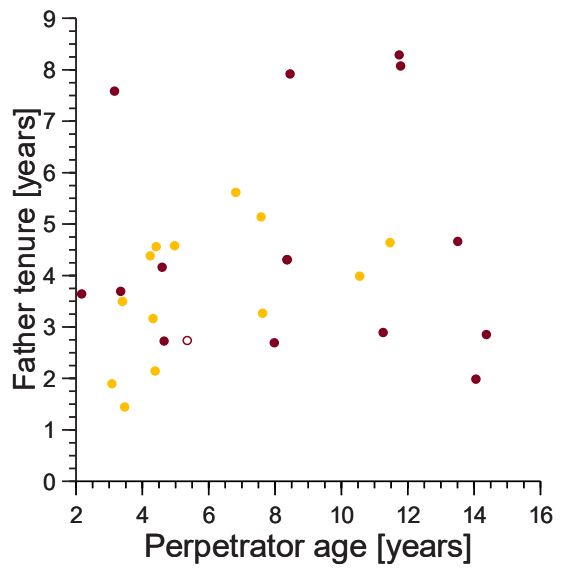

FIGURE 6 | The tenure of the fathers of cubs lost to violent attacks (burgundy) and maternal neglect (amber) on the date when the cub was conceived in relation to the age of the female perpetrator of the violence on the date of cub death (burgundy) or the age of the mother at conception of the victim if the victim died from fatal maternal neglect (amber). Filled symbol: immigrant males, open symbol: natal male.

the same genetic father. For 32 infanticides by violent attack for which we knew or suspected the identity of the female perpetrator, we identified in 15 cases the genetic father of both the victim of the attack and the genetic father of the dependent

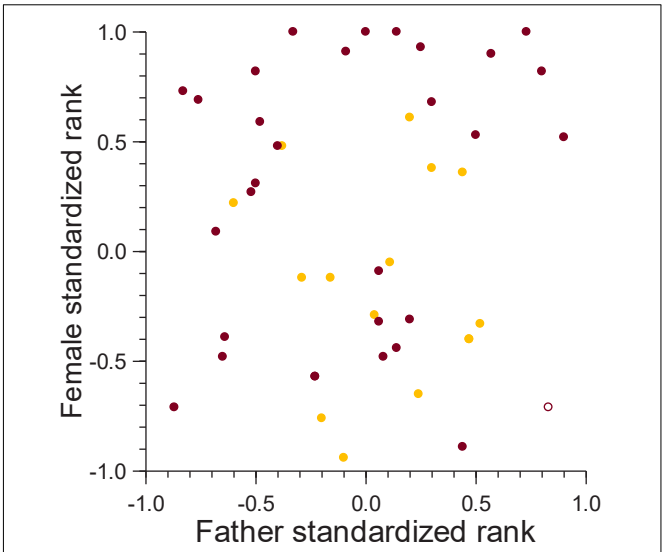

FIGURE 7 | The standardized rank of mothers of cubs lost to violent attacks (burgundy) and maternal neglect (amber) in relation to the standardized rank of their fathers at conception of the victim. Filled symbol: immigrant males, open symbol: natal male.

offspring of the perpetrator when it killed the victim. There was not a single case in which the victim of infanticide and the offspring of the female perpetrator shared a father.

DISCUSSION

Despite substantial research on within-group infanticide in social mammals, to our knowledge this is the first study to gauge the reproductive cost of infanticide by adult females to breeding males in their group. Based on more than 30 years of data, our study provides evidence that infanticide by adult females in spotted hyena clans significantly reduced the reproductive success of breeding males whose offspring died of violent attacks or fatal maternal neglect. Because our recorded paternity losses incurred by males for both these sources of infanticide are probably minimum estimates, actual losses from infanticide are likely to be substantially larger. Both these sources of infanticide generated sexual conflict between breeding males whose reproductive success was reduced and adult females that comitted infanticide. We show that violent attacks on cubs by adult females during periods of social instability (aggressive conflict amongst competing females at the top of the female dominance hierarchy, **Figure 1**), have a larger negative impact on the reproductive success of affected males, thus generate a higher level of sexual conflict than cub deaths caused by fatal maternal neglect (**Tables 1**, **2**). We found little evidence that breeding males have effective counterstrategies against infanticide by females. This suggests that breeding males are mostly powerless in preventing the detrimental fitness outcome of infanticide by females in their clan.

Incidence of Infanticide by Violent Attacks

Research on infanticide in large wild mammals, such as the spotted hyena, is challenging because observations of violent infanticide are rare, attacks are swift, and evidence of infanticide, including material for genotyping the victim, may be swiftly consumed. For these reasons, our results on the fitness cost to fathers of violent attacks by adult females on the cubs they sired are minimum estimates, and the true effects on the fitness of fathers are likely to be substantially higher. A long-term study on infanticide in a population of spotted hyenas in Kenya also concluded that observed incidences of infanticide are likely to underestimate the true occurrence of this behavior (Brown et al., 2021).

Our results indicate that violent infanticide accounted for the death of between 3.3–5.7% of cubs born during our study. We predicted that periods of social instability in our three study clans would be associated with an increase in the incidence of violent infanticides. Our results are consistent with this prediction as periods of social instability were associated with a higher rate of offspring mortality (**Table 1**) than periods of social stability, and this increase was driven by the records of observed and suspected infanticides. Even during these short periods of social instability, there was a substantial proportion of offspring mortality for which the cause was unknown, which may have included undetected cases of infanticide.

Loss of Paternity to Infanticide, Sexual Conflict and Female Social Status

As predicted, violent attacks by adult females represented a larger reduction of the rate at which breeding males produced offspring than fatal maternal neglect (**Table 2**). This suggests that violent attacks are a more important source of sexual conflict between adult female perpetrators and the genetic fathers of killed cubs than fatal maternal neglect. Fathers that lost cubs to violent attacks by adult females produced fewer offspring that survived to adulthood than those who did not (**Figure 2**). Thus violent attacks on cubs by females reduced fitness of affected breeding males, and was a source of sexual conflict between infanticidal females and affected breeding males. Infanticides by violent attack were perpetrated by adult females from a wide range of ages and the genetic fathers of their victims held widely different breeding tenures (**Figure 6**).

Violent attacks mostly killed cubs sired with higher-ranking females (**Figure 7**). As offspring of mothers above median rank had a higher survival to adulthood than those with mothers below median rank (Holekamp et al., 1996; Hofer and East, 2003; Höner et al., 2010; Ferreira et al., 2019), losses of offspring sired with high-ranking females may be compensated to some degree by the higher likelihood of survival to adulthood of other offspring sired with higher-ranking than lower-ranking females.

Female dominance hierarchies within spotted hyena clans can be stable for long periods, but periods of social instability do occur in our study population (Goymann et al., 2001) and we identified numerous periods of social instability in our three main study clans during the study (58 periods in total). As predicted, periods of social unrest were associated with intense fights between high-ranking females in competing coalitions (**Figure 1**) and increased cub losses to violent attacks by adult females (**Table 1**). These attacks mostly involved offspring sired by breeding males below or around median rank with high-ranking mothers.

The fission-fusion structure of clans is accentuated in our study population by long-distance foraging trips outside the clan territory. Low-ranking females meet the high energetic costs of lactation by allocating a large proportion of their protracted nursing period to commuting long distances between the clan communal den and distant locations containing large numbers of migratory ungulates (Hofer and East, 1993c; Gicquel et al., 2022). As commuting results in lengthy maternal absence intervals from milk-dependent cubs (Hofer and East, 1993c) and a reduced milk intake by cubs (Hofer et al., 2016), we expected males that sire offspring with low-ranking females should be more likely to lose paternity to maternal neglect. Evidence that long-distance commuting by lactating low-ranking females might undermine maternal body condition and reserves, thereby increasing the chance that a female might abandon a litter, is supported by evidence of significantly higher intestinal parasite burdens in low-ranking than high-ranking lactating females (East et al., 2015). As expected, infanticide by fatal maternal neglect resulted in the death of more offspring sired with lower-ranking than higher-ranking females, and we have no evidence that females at the top of the hierarchy (those above standardized ranks + 0.7) committed infanticide by fatal maternal neglect (**Figure 7**).

We predicted that strong female mate-choice would constrain any pattern of male mate-choice that might reduce paternity losses to infanticide. We expected females to avoid the fitness cost associated with inbreeding with close male relatives by choosing sires that started their reproductive tenure after the female was born (Höner et al., 2007). In line with this, most mothers of victims of infanticide (by violent attack and fatal maternal neglect) had selected a sire that adhered to the expected pattern of female mate-choice (**Figure 5**, points to the right of the dotted line). From this female mate-choice rule, we expected a positive association between female perpetrator age on the date of cub death due to fatal maternal neglect and the tenure of the genetic fathers, as was the case. We would not expect an association between the age of female perpetrators of violent attacks on the date of infanticide and the tenure of the fathers of the cubs they killed, and indeed there was no such association (**Figure 6**).

It is unlikely that young mothers are proficient in long-distance commuting trips to distant migratory herds when rearing their first few litters (East et al., 2015). As a result, the first few litters of low ranking-females may be particularly prone to infanticide by fatal maternal neglect, as young, inexperienced mothers have to fuel lactation for many months by long-distance foraging that can involve regular 140 km round trips (Hofer and East, 1993b). Consistent with this suggestion, most infanticides by fatal maternal neglect involved younger rather than older mothers (**Figure 6**). This suggests that by perpetrating infanticide by fatal maternal neglect, inexperienced breeding females caused sexual conflict with relatively short tenured, mostly low-ranking males. By contrast, and regardless of their age, adult females of

a wide range of ages generated conflict with males that differed widely in their length of tenure (and hence social status) by perpetrating infanticides through violent attacks (**Figure 6**).

Possible Male Counterstrategies to Infanticide by Adult Females

Although various counterstrategies against violent infanticide have been reported in mammals, we predicted that few if any would be implemented by male spotted hyenas because of female social dominance, strong female mate-choice and prolonged offspring dependence on lactation and the negligible contribution by fathers to rearing offspring.

The defense of offspring from violent infanticide, by counterattacking perpetrators and by forming alliances with other individuals to increase protection of offspring, has been reported in several species (Packer and Pusey, 1983; Agrell et al., 1998; Fruteau et al., 2010; Palombit, 2015). Our long-term observations provided no evidence of male spotted hyenas forming alliances to prevent violent infanticide or counterattacking adult females during or shortly after they perpetrated violent infanticide. There are several reasons why males would not be expected to do this. The fission-fusion structure of spotted hyena clans substantially reduces the chance that fathers would be present at the communal den to defend their offspring from a violent infanticide. In our long-distance commuting population, high-ranking breeding males are present at the communal den more often than other breeding males (East and Hofer, 1991), but even top-ranking males are much more frequently absent from dens than lactating females, which in turn can be absent for up to 9 days (Hofer and East, 1993c). Low-ranking males typically visit communal dens infrequently and only for short periods (East et al., 2013), thus their chance of being present at the communal den when violent infanticide of their offspring occurs is very low. High-ranking females aggressively harass, chase and even carry (by their necks) cubs of lower-ranking females at the communal den. Breeding males witness these acts, plus the attempts by mothers to assist their cubs, but we have never observed breeding males intervening, on their own or to support mothers, to protect cubs. When violent infanticides occur, the action of the perpetrator is typically swift, as perpetrators grab and crush the skulls of their victims, as also reported in other populations (Brown et al., 2021). Given that victims are mostly swiftly dispatched, an aggressive counterattack by a father would be very unlikely to prevent the death of its offspring. Finally, during periods of social instability when conflict between females is intense, breeding males—including high-ranking ones—usually keep themselves away from the communal dens, in order to avoid being targeted by aggressive acts of females (East and Hofer, unpublished observations).

Dispersal is a counterstrategy typically used by females in some mammals to avoid violent infanticide (Pusey and Packer, 1994; Sterck and Korstjens, 2000; Zhao et al., 2011). We assessed whether strategic timing of secondary dispersal by breeding males reduces their chance of paternity loss to infanticide by adult females, as we expected the likelihood of such losses to increase with a male's breeding tenure. As expected, males which lost offspring to violent attacks or to fatal maternal neglect had longer total tenures, by approximately 2.5 years, than those that did not. This difference was significant for males with losses to violent attacks but not for males with losses caused by fatal maternal neglect. In the latter cases, the lack of significance is probably best explained by the small sample size, thus the statistical power of the test was too small to demonstrate significance. In principle, our result are consistent with the idea that secondary dispersal to another clan at a shorter breeding tenure than that held by males who suffered losses is a potential counterstrategy, but it is not one that is guaranteed to provide fitness benefits.

This is because secondary dispersal entails additional costs to those incurred when males remain in their current clan. These include the costs of dispersal and integration into a new clan and the losses of relationships formed with adult females during the years of tenure in the former clan (East and Hofer, 2001; Szykman et al., 2001). These negative effects of secondary dispersal on male fitness may be greater than those of infanticide by females in the former clan. Additionally, access of immigrant males to food in their clan territory increases with social status (Frank, 1986), and as this is determined by the immigrant male social queue, access to food in the clan territory also increases with male tenure. By placing an immigrant male at the bottom rank in the dominance hierarchy, secondary dispersal would therefore result in reducing access to food in the current clan territory. In our long-distance commuting population, this would also require the male to spend a greater proportion of the year on long-distance commuting than in its previous clan, thereby reducing time spent in the territory of a new clan, building relationships with females and locating females in estrus. As males of a wide range of tenures experience reproductive losses from infanticide (**Figure 6**), it is doubtful that secondary dispersal substantially reduces uncertainty about the future prospect of losses from infanticide by females. It therefore does not appear to be an effective counterstrategy to reduce the fitness cost of infanticide by females.

A third counterstrategy could be bet-hedging, in terms of males siring cubs with numerous females to ensure that potential losses of paternity from infanticide are compensated by the survival of offspring sired with other females. Effective application of such a counterstrategy is probably constrained by strong female mate-choice (Engh et al., 2002; East et al., 2003; Höner et al., 2007). The extensive fission-fusion nature of clans, in particular the long-distance commuting by both adult females and breeding males that, limits the number of females in estrus which a breeding male is likely to encounter when it is present in the clan territory. As females apparently confuse paternity of their offspring by copulating with multiple males when in estrus and when not in estrus, and—as genetic paternity analyses reveal—only a limited number of male copulations that occur are detected (Engh et al., 2002; East et al., 2003), observed male copulations do not accurately reflect genetic paternity. For these reasons, a test of whether males that were observed to copulate with multiple females lose fewer offspring to infanticide or have overall more surviving offspring than males that do not is not possible in our study system.

Could males flexibly respond in terms of bet-hedging if they recognized their offspring and were aware that they died from

infanticide? If males could recognize their offspring, spreading their risk through bet-hedging might make sense regardless of the cause of death, so this would not be specific to offspring lost to infanticide. As argued above, the fission-fusion nature of Serengeti clans and the commuting system would ensure that there is a low likelihood that males would witness their offspring's death, regardless of the cause of death. Confusion of paternity (East et al., 2003) ensures that males cannot use their own copulation success to know which cubs at a communal den they have sired. Alternatively, could males directly recognize their own offspring? There is no behavioral evidence that males recognize the offspring they sire (Van Horn et al., 2004) and even if males could recognize their offspring and/or were aware that their offspring had suffered infanticide, we found no evidence that they sought to increase the number of females they sired offspring with. Rather, males sired offspring with similar numbers of females, regardless of whether they had or had not lost paternity to infanticide by females. This result suggests that bet-hedging to avoid losses from infanticide is unlikely to be important for any breeding male in our population.

A fourth strategy might be that males choose to or avoid siring cubs with specific females. Did they do so? In the cases when we knew both the genetic fathers of cubs that died from violent attacks and the identity of the female perpetrator, the victims were not related through the paternal line to the offspring of the perpetrators and the males which lost cubs did not sire offspring with the perpetrators before or after the losses from violent attacks. This might be the fortuitous outcome of the large group sizes of our study clans, with a large number of breeding females (between 15 and 50) and a similar number of males (Olarte-Castillo et al., 2016), so even in the absence of mate-choice and random mating, the likelihood of any one combination of mating partners is low. This result therefore does not provide evidence of active choice or avoidance of females by males.

Furthermore, the slow rate of reproduction of females caused by high post-natal maternal input throughout the long lactation period (Hofer et al., 2016) probably creates a skewed operational sex ratio in favor of breeding males to females in estrus. To sire offspring, males must successfully compete for mating opportunities in a system where females exercise strong mate-choice, hence male counterstrategies to infanticide are constrained by this framework. Given the relatively low cost to males of siring offspring because of their negligible contribution to the rearing of offspring (**Table 2**), it is doubtful that breeding males reject any opportunity of mating offered by a female, even if the prospects of the resulting offspring reaching adulthood is low, such as offspring sired with low-ranking, inexperienced females (**Figures 6**, **7**).

Instead, the best option for males to maximize reproductive success, and thereby minimize the possible consequences of paternity losses from infanticide is probably to start their breeding tenure in the clan containing the largest number of females likely to accept them as a mate. This would be the clan with the largest number of young females, which on occasion might be their own natal clan. If males do so, they substantially increase their reproductive success (Höner et al., 2007), which may compensate to some extent potential reproductive losses to infanticide.

Our study reveals that infanticide by adult females reduces the fitness of affected breeding males and generates sexual conflict to which breeding males apparently have no effective counterstrategies. In this respect, female perpetrators exercise power to obtain an outcome that is thought to be advantageous to them and costly to affected breeding males. Currently, little is known about the fitness costs of infanticide by females to breeding males in other social mammals. We hope our study encourages further research on this topic.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

This study was approved by the Committee for Ethics and Animal Welfare of the Leibniz Institute for Zoo and Wildlife Research (2018-11-01).

AUTHOR CONTRIBUTIONS

ME and HH designed the study and wrote the manuscript. ME, DT, SB, SM, and HH collected the data. ME, DT, and HH conducted the analysis. All authors edited the manuscript.

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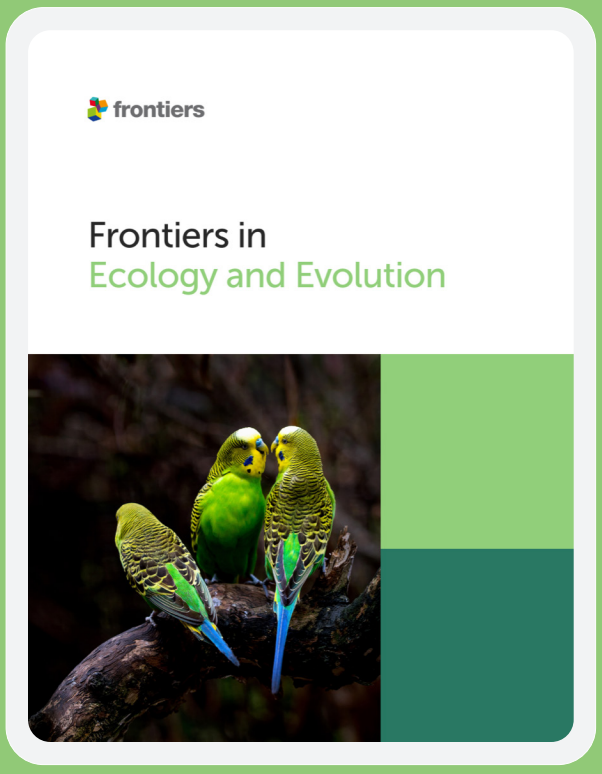

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