CORONAVIRUS DISEASE (COVID-19) AND ITS PSYCHOBEHAVIORAL CONSEQUENCES

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Table of Contents

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EDITORIAL
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Editorial: Coronavirus Disease (COVID-19) and Its Psychobehavioral Consequences

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Editorial on the Research Topic

Coronavirus Disease (COVID-19) and Its Psychobehavioral Consequences

The presence of pathogens has imposed constant threats to human survival and reproduction. Selective pressures exerted by pathogens have shaped our array of immune functions—including physiological, psychological, and behavioral immune systems. Pathogens and epidemics have plagued humankind and our ancestors from their dawn, yet despite advances in hygiene and medicine, these threats remain with us today. In 2020–2021, pathogens have become a particularly salient part of everyday life as we have faced a worldwide outbreak of SARS-CoV-2.

We launched this Research Topic with the specific recognition that evolutionary approaches, which acknowledge the biological forces shaping and underlying human cognition and behavior, are uniquely positioned within psychology and behavioral science to offer insights on the responses to and outcomes of the COVID-19 pandemic. The collection of 14 articles published in this Research Topic has surpassed our original vision, introducing diverse evolutionary perspectives on various aspects of the COVID-19 pandemic. Varella et al. captured the importance of an evolutionary approach to COVID-19 by stating that "Everything in pandemics is stamp collection except in the light of evolution." Research focused on pandemics without an explicit evolutionary framework can also be very valuable as it can offer the pieces of the jigsaw puzzle that evolutionarily oriented researchers need to integrate in their quest to understand the bigger picture.

GAME-THEORETICAL APPROACHES TO THE COVID-19 PANDEMIC

Cooperation and compliance with pandemic safety regulations are important facets of a public health response to limiting the spread of a virus such as SARS-CoV-2. These aspects of a public response to a pandemic can be fruitfully analyzed via evolutionary game theory. According to this approach, public health is a *public goods game*, and its maintenance depends on the contributions of a critical number of individuals, as discussed by Yong and Choy. The authors noted that this leaves room for defectors who can pursue their own interests without contributing to the common good of public health during the pandemic. Such free-riders can enjoy the benefits of decreased health risk from others' compliance with health policies despite failing to contribute to—or even

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undermining—public health themselves. Their non-compliance behavior may, when detected, also be punished for example through legal enforcement and penalties, as discussed in detail by Yong and Choy.

SEX DIFFERENCES IN PANDEMIC LEADERSHIP

This scenario constitutes a public goods dilemma where various game-theoretic strategies may bear different payoffs according to the strategies of other "players" in the game, including the kinds of top-down policies that are implemented to curb the spread of the virus and to punish defectors. Luoto and Varella's review article on pandemic leadership established that female-led countries were better at minimizing COVID-19-related deaths in 2020. This outcome likely arose because of female leaders' stronger empathy, higher pathogen disgust, health concern, care-taking orientation, and dislike for the suffering of other people, as suggested by existing research on psychobehavioral sex differences in other domains (reviewed in detail in Luoto and Varella). Societal leadership and top-down policies comprise important factors that can shape human behavior so that the collective good of public health is prioritized over selfish individual actions, effectively overriding our evolved psychological mechanisms for selfish behavior so that we can reach a higher-level societal goal. As shown in Luoto and Varella's review article, male and female leaders, on average, placed slightly different emphases on different outcomes during a pandemic. Thus, men and women can have somewhat different "strategies" as players in the public goods "game" of the pandemic, in line with their evolved psychobehavioral dispositions.

PROSOCIAL VS. SELFISH BEHAVIORS IN A PANDEMIC CONTEXT

Dinić and Bodroža demonstrated the crucial role of empathy and the importance of prioritizing higher-level societal goals during the COVID-19 pandemic. They studied the effect of six prosocial personality tendencies, selfishness as an antisocial personality trait, fear related to the pandemic, and empathy toward most vulnerable society members as determinants of protective behaviors against COVID-19 (e.g., washing hands, wearing a mask, and physical distancing). Altruism had a positive effect and selfishness had a negative effect on protective behaviors. Thus, an antisocial and selfish strategy can decrease the chances of personal survival and the survival of group members. Increased fear related to the pandemic had an important effect on people's protective behaviors. However, fear had no significant moderator effect in the relationship between personality traits and protective behavior. At the same time, the authors found that empathy acted as a mediator, helping to effectively promote health-responsible behaviors.

Other articles in the Research Topic have analyzed the characteristics of those more likely to act selfishly in such a "public goods dilemma" as the COVID-19 pandemic. Corpuz et al. reported that individuals with fast life history strategies had lower self-reported adherence to pandemic precautions, lower willingness to donate plasma, and lower endorsement of mandatory COVID-19 vaccination. This is consistent with the general idea of fast life history strategies being associated with bioenergetic investment in reproduction over longevity and health. Varella et al. combined this approach with their *eveningness epidemiological liability hypothesis*, which posits that evolved propensities for nocturnal activities—which manifest in contemporary life in activities such as restaurant dining and going to bars and nightclubs—might have become a dangerous liability against epidemiological control partly because SARS-CoV-2 persists in aerosols much longer during the night and indoors than outdoors during the day. Thus, life history strategies and chronotype, together with sex, can explain some of the individual differences in non-compliance with pandemic safety measures, although Varella et al.'s *eveningness epidemiological liability hypothesis* still requires direct empirical testing.

Norton et al. reported that during the early stages of the pandemic, Australians matched their behavior to perceived social norms, which were used to infer the seriousness of COVID-19. More specifically, there was a positive association between people's perceptions of others' adherence to social distancing recommendations, their perceptions of the seriousness of COVID-19, and their own adherence to social distancing recommendations. This finding has interesting implications for game-theoretical scenarios related to the pandemic, suggesting the existence of a "tit-for-tat" strategy. Self-reported adherence to safety measures was also positively linked to anticipated shame and to perceptions of the moral wrongness of non-adherence, indicating that the threat of social punishment may in part motivate adherence to pandemic safety guidelines—a kind of culturally sanctioned behavioral immune system.

BEHAVIORAL IMMUNE SYSTEM

This kind of culturally enforced behavioral immune system is an important part of the collective fight against the pandemic because at the individual level, the SARS-CoV-2 virus can evade many of our evolved contagious disease avoidance tendencies. After all, even asymptomatic carriers of the virus are contagious, and most infected individuals have only very mild or no symptoms at all (Varella et al.). The absence of disease cues leads to an attenuated or even absent activation of contagious disease avoidance mechanisms, which can contribute to non-compliance with the pandemic safety measures, as noted by Varella et al. Ultimately, this highlights the need for top-down measures from health authorities and political leaders to eliminate the virus.

Comparisons of pre-pandemic behavioral measures with those acquired during the pandemic nevertheless showed heightened activation of individual-level behavioral immune system across three studies in this Research Topic. Studying Croatian populations, Hromatko et al. reported that preferred interpersonal distances, pathogen disgust, and germ aversion were higher during the pandemic than before. Conservatives and women were more likely to agree that the government

should severely punish those who did not adhere to COVID-19 preventive measures (conversely, in the US, participants who reported being more conservative were less likely to endorse precautions surrounding COVID-19, as reported by Corpuz et al.). Furthermore, Croatian islanders had higher preferred distances with strangers and showed higher negative emotions toward foreigners than mainlanders did, suggesting higher behavioral immune system activation in islanders. This may arise from their more isolated geographical location, which makes them more vulnerable if a new pathogen finds its way into the population because isolated populations are typically shielded from exposure to various pathogens. Hromatko et al. concluded that when cues of risk of infection are high, xenophobic attitudes might serve as a steering wheel that keeps one from coming into close contact with possible disease carriers.

Models of disgust as functionally important for disease avoidance argue for its flexibility as disease circumstances change. Few tests of this idea exist. Stevenson et al. used the occurrence of the COVID-19 pandemic and data sets from prior studies to test this idea. They showed that people during the pandemic—a time when infection transmission is notably increased—reported heightened disgust sensitivity and germ aversion (a related construct) compared to similar samples from just a few years ago. They also showed that across the samples, while sex differences existed, the differences were consistent. Furthermore, they found that impulsivity was rather consistent across the samples. The consistency in sex differences and the similarity in impulsivity bolster the authors' conclusion that the increase in disgust sensitivity is related to the pandemic rather than reflecting nuances of the samples.

Miłkowska et al. also examined disgust fluctuations pre- and post-pandemic, examining two demographically similar cohorts of Polish women. Results partially supported the hypothesis that disgust increased during the early pandemic (April–May, 2020). Women from the pandemic cohort rated photographs of infection sources as more disgusting, scored higher in contamination sensitivity, and reported lower moral disgust than the pre-pandemic cohort. Cohorts did not differ in pathogen disgust. However, the pandemic cohort women reported higher state anxiety, which was positively associated with photograph disgust, contamination sensitivity, and pathogen disgust. As Hromatko et al. noted, the behavioral immune system therefore is a contextually sensitive pathogen detection and avoidance system which partially underlies social cognitions and patterns of interpersonal approach/avoidance motivations.

This view is further supported by the finding that the COVID-19 threat did not strengthen the relationship between disgust and homonegativity. Szymkow et al. reported a positive correlation between sexual disgust and negative attitudes toward gay men and lesbians in a Polish sample. However, pathogen disgust did not predict homonegativity, nor did homonegativity increase during the pandemic. This suggests that the behavioral immune system is not hypersensitive to homosexuality in the COVID-19 context. In a *sexual* context, in contrast, homonegativity was associated with increased disgust—possibly because of the association between sexually transmitted diseases and homosexuals, as discussed in Szymkow et al.

Despite the results showing increased behavioral immune system activation in the COVID-19 context, Gassen et al. reported that while participants with higher clinical risk for severe COVID-19 (calculated using weighted measures of demographic characteristics such as age, BMI, and sex, and pre-existing conditions such as cardiovascular disease or cancer) acknowledged their greater likelihood of experiencing severe illness if infected, they actually reported lower perceived likelihood of becoming infected. While such unrealistic optimism might improve the short-term psychological well-being of those at high risk, it can also lead to a level of carelessness that unnecessarily increases the risk of infection and severe COVID-19 for such high-risk individuals. As Gassen et al. noted, while optimism bias has evolutionary origins, it does not mean that unrealistic optimism is an "optimal" strategy in every situation, particularly when individuals experience a novel source (or scale) of risk that was not present in the environments under which optimism biases may have evolved. This perspective highlights the utility of the evolutionary mismatch hypothesis in the COVID-19 context, as discussed in detail by Varella et al.

REPRODUCTIVE DECISION-MAKING, POSTNATAL DEPRESSION, AND EATING BEHAVIORS IN A PANDEMIC CONTEXT

The mismatch perspective becomes even more relevant when considering large-scale existential threats like climate change. Gordon examined the relationships between mortality threats and reproductive decision-making using a life history theory framework. Extrinsic mortality threats (external threats to individual survival) are linked to greater reproductive effort, while existential threats (external threats to species survival) are relatively novel and remain unexamined in life history research. Extrinsic threat from COVID-19 (knowing those hospitalized or dead) was positively associated with ideal number of children. Existential threat (measured via climate change beliefs) was not clearly associated with reproductive decision-making. Taken together, these results provide evidence that reproductive decision-making shifts are functionally attuned to historically recurrent mortality threats like pandemics, but not to more novel, species-wide threats like climate change.

Myers and Emmott explored how new mothers' social communication impacted postnatal depressive symptoms during London's first pandemic lockdown. The authors acknowledged that while humans are cooperative childrearers, pandemic mandates have severely limited in-person contact. Seeing more social network-members in person or communicating more with those not visited with was linked to fewer depressive symptoms in new mothers. However, contact with a greater proportion of relatives was positively associated with depressive symptoms, suggesting that kin may have sought to visit particularly those mothers who needed it the most. Rich qualitative data in Myers and Emmott's article also illustrated themes in COVID-19 lockdown experiences. For example, participants wrote about benefits of the lockdown, like increased time to bond with their baby. They also illustrated lockdown burdens, like the obligation

to "constantly mother," inadequate social support, and missed developmental opportunities for their children. A substantial number of women in the sample met diagnostic criteria for postnatal depression, reflecting a rise in rates seen in other samples collected during the pandemic. Taken together, these results suggest that lockdown has negatively affected mothers' well-being and that peer network members' support is needed to help buffer these impacts.

Not everything is necessarily worse during pandemics. Freitas et al. conducted a longitudinal study before and during the pandemic focusing on anxiety, premenstrual symptoms, and eating behavior in young Brazilian women. They found that anxiety/stress, uncontrolled and emotional eating, and desire for sweet and fatty food were higher before the pandemic. The traditional food, social interaction, and support of living back together in one's family home might buffer people from the stresses of the pandemic, particularly in small-city contexts.

CONCLUSION

This Research Topic has gone a long way into offering new high-quality theoretical insights and empirical findings stemming from an integrative evolutionary approach that can contribute to the way psychological and behavioral sciences predict, model, and deal with the current and future pandemics. Forty-three authors contributed to this Research Topic, reporting findings from Australia, Brazil, Croatia, Poland, Serbia, the UK, and the US. We thank the authors, reviewers, and external editors who accepted the challenge of approaching the current COVID-19 pandemic from an evolutionary perspective. It was not an easy task because there is limited existing evolutionary research on pandemics, but this article collection provides examples of the many ways in which evolutionary principles can help advance psychological and behavioral science applied in a pandemic context.

AUTHOR CONTRIBUTIONS

All authors contributed to writing this article.

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BRIEF RESEARCH REPORT
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Life History Orientation Predicts COVID-19 Precautions and Projected Behaviors

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The ongoing Coronavirus disease (COVID-19) pandemic has had a devastating impact worldwide. It is unclear as to what one expects during the "post-peak" and "post-pandemic" periods in terms of: (1) continued adherence to precautionary measures (e.g., wearing a mask) and (2) behaviors during these periods pertaining to widespread (anticipated) medical solutions that can buffer subsequent waves (e.g., vaccination and donating plasma). In this study, we examine predictors of individual differences in attitudes and behaviors with regard to the COVID-19 pandemic and the months moving forward. Of the factors that contribute to how one might navigate the pandemic – a source of elevated environmental threat – life history orientation may play a crucial role. In this study, participants (n = 209) indicated their agreement with items on attitudes toward COVID-19 precautions and medical solutions that can buffer subsequent waves. In all models, we found significant positive relationships between one's slow life history orientation and their self-reported adherence to precautions and endorsement of medical solutions. This effect was detectable even after controlling for factors related to political conservatism and personal experience with deleterious events as a result of the pandemic. Discussion includes reflection on the main finding, demographic variables, as well as the relationships uncovered among the modeled covariates (e.g., social conservatism, political conservatism).

Keywords: COVID-19, coronavirus, life history theory, pandemic, conservatism

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INTRODUCTION

The ongoing Coronavirus disease (COVID-19) pandemic has – in the United States alone – infected over 1.5 million people and has claimed the lives of more than 100,000 individuals (CDC as of June 1, 2020; cdc.gov/coronavirus/2019). For some, this information is sufficient to cause alarm and bring attention to things one can do to avoid infection and/or infecting others. Yet, there lacks uniform agreement as to what to expect during the "post-peak" and "post-pandemic" periods in terms of: (1) continued adherence to precautionary measures (e.g., wearing a mask) and (2) behaviors during these periods pertaining to widespread (anticipated) medical solutions that can buffer subsequent waves (e.g., vaccination and donating plasma). We explore these gaps in detail using data collected at the height of the pandemic.

Life History Theory

When confronted with challenge or environmental uncertainty, one's response is not arbitrary. At the core of life history theory (LHT)[1] is the appreciation for the enduring influence of information in early development being utilized as a forecast in service of meeting the environmental demands of later development (Ellis and Bjorklund, 2012). Life history strategies exist along a "slow" to "fast" continuum – terms that indicate the relative tempo of one's development and reproduction (Ellis and Bjorklund, 2012). Slow strategists are characterized by stable relationships (kin, romantic, social exchange partners) and a propensity for long term planning, risk averseness, and prosocial behavior (Del Giudice and Belsky, 2011). When the early environment presents itself as safe and stable, one can be assured that their life (and the lives of those around them) will extend well into the future. Fast life histories are marked by the opposite pattern. Faced with the risk of premature death and forced to navigate a social environment with exploitative agents, fast strategists accelerate development and develop an orientation toward succeeding in the here and now. These include risk taking, short term decision making, and decreased prosociality; these strategies are highly adaptive in environments where life is uncertain (Ellis et al., 2003; Simpson and Belsky, 2008; Del Giudice and Belsky, 2011).

In higher risk environments, one's "fast" life history strategy will be comprised of being less averse to risk, more present (as opposed to future) oriented, and less affiliative (de Baca et al., 2016; Zhu et al., 2018; Lu and Chang, 2019). This self-centered, antagonistic social strategy helps the individual prepare for competing with others that may have divergent interests in their own immediate survival. Under risky and unpredictable environmental conditions, one must attend to immediate survival needs and discount future interactions and conspecific cooperation.

In lower risk environments, one can execute social strategies that are more mutualistic as one can rely on the convergent interests of those in a group (Figueredo and Jacobs, 2010; Chang and Lu, 2018; Lu and Chang, 2019). In environments that are more predictable, slow strategists can orient toward long term planning and more affiliative social behaviors (Ellis et al., 2009; Figueredo et al., 2018). One can afford to invest in a social orientation that includes coexistence and cooperation with others to maximize resource acquisition through collaboration (Chen and Chang, 2016; Zhu et al., 2018, Zhu and Chang, 2019).

Predictions

There are differences in the levels of attitudinal endorsement for behaviors that can reduce the impact of COVID-19 (e.g., prolonged social distancing, masks in public) and those that can help buffer the impact on mortality (e.g., vaccines, plasma donation from recovered) in the long term. As detailed above, slow life history strategists demonstrate a social orientation toward longer term planning, more affiliative social behaviors, and being risk averse. *We hypothesize that those who demonstrate a slow life history strategy will have higher levels of attitudinal endorsement for behaviors that can reduce the impact of COVID-19.*

Similarly, we hypothesize that slow life history strategists would be more likely to endorse more affiliative behaviors such as donating plasma and vaccine administration. We include covariates where appropriate to isolate the strength and direction of this relationship. These include demographic variables (age, sex, religion, geographical location) as well as personal experience with pandemic-related events and political conservatism – factors that play a role in attitudes and behavior during pandemics (e.g., Navarro et al., 2006; Mesch and Schwirian, 2015; Barrios and Hochberg, 2020).

METHODS

Overview and Study Design

This study was explicitly designed in response to the COVID-19 pandemic. Participants contributed data between May 9, 2020 and May 19, 2020[2]. All materials and procedures were reviewed and approved by the University's Institutional Review Board (IRB).

This study utilizes a convenience sample from Amazon's Mechanical Turk (MTurk), an online survey tool. MTurk is particularly well-equipped to collect data from participants remotely. MTurk participants demonstrate psychometric equivalence to other data collection methods (Paolacci et al., 2010; Arditte et al., 2016; Hauser and Schwarz, 2016; Kees et al., 2017; McCredie and Morey, 2019).

Utilizing G*Power (Erdfelder et al., 1996), we determined an optimal sample size for this fixed model with an anticipated "small effect" and up to six predictors (power = 0.95) would be at least n = 146. The outcome measures utilized in this study have not been deployed together; we were conservative with our prediction of effect size when calculating *a priori* sample size.

Participants were presented with a consent form and granted consent prior to seeing any items from the survey. At the conclusion of one's participation, they were compensated $11.50 for completion of the study materials, which included additional measures not examined in the present study (573 total items; mean response time = 77 min).

Participants

Participants (n = 209) contributed data between May 9, 2020 and May 19, 2020. The sample was disproportionally male (55.1%). Participants ranged from 19 to 60 years of age, with a mean age of M = 33.4 years (SD = 11.4). The majority of participants identified as European American (72.5%), followed by Asian American (9.7%), African American (7.3%), Hispanic or Latino/a (6.1%), Native American (1.5%), and Other (0.9%). In terms of religion, this sample lacked the heterogeneity (i.e., Agnostic/none = 53% and Christian, 40%; maximum of n = 2 in remaining groups) to

[1]As it is utilized contemporarily in research on, for example, human psychology and psychobiology.

[2]World Health Organization declared COVID-19 a pandemic on March 11 (World Health Organization COVID-19 Landing, 2020) and the United States declared a state of national emergency on March 13.

form any more than two groups and, as a result, religion will be treated as a binary variable. The median income of this sample was reported as $45,000–$60,000 annually. In terms of education, 62.2% of this sample held at least a bachelor's degree. Based on census demarcations (see "Demographic Covariates" section), the geographical distribution of participants in this study were: Northeast (n = 54), South (n = 46), Midwest (n = 41), Pacific (n = 26), and Mountain (n = 6).

Materials

Life History Strategy

The Life History Battery Short Form (LH-SF; Figueredo et al., 2015) assesses several domains of social and sexual behavior that reveal an individual's "K-factor" – the degree to which one adopts a fast versus slow life history strategy. The LH-SF is a psychometric measure of life history orientation. Items ask about cognitive and behavioral indicators of one's life history orientation. For example: "When faced with a bad situation, I do what I can to change it for the better" and "While you were growing up, how much love and affection did your biological father provide." Participants respond to each question on a Likert scale ranging from strongly disagree (−3) to strongly agree (+3). The measure demonstrates convergent validity (Olderbak et al., 2014) and Cronbach's alpha is consistently adequate in the literature ($\alpha > 0.70$) (see Olderbak et al., 2014).

The LH-SF produces a total (summed) value across all items. In the current sample, reliability was adequately high as well ($\alpha = 0.91$ across 42 items). Life history orientation was normally distributed (skewness = 0.03, SE = 0.17; kurtosis = −0.47, SE = 0.34). This predictor variable (M = 50.94, SD = 30.23) was treated as a continuous variable in all models. Higher values on this measure indicate a *slower* life history strategy.

COVID-19 Deleterious Events

The Epidemic-Pandemic Impacts Inventory (EPII; Grasso et al., 2013) was developed to learn more about how the pandemic has changed people's lives. For each statement, participants indicate whether the pandemic has impacted the self or others in the household (or both) for each item. The EPII asks participants to self-report on the occurrence of stressors in various domains of personal and family life: *"We would like to learn how the coronavirus disease pandemic has changed people's lives. For each statement below, please indicate whether the pandemic has impacted you or your family in the way described.* The full EPII is 107 items ($\alpha = 0.82$ in current sample) distributed through 11 subscales. For the current study, we excluded the subscale "positive events" as our interests were on the influence of experiencing deleterious events. The full EPII can be found online: health.uconn.edu/psychiatry/child-and-adolescent-psychiatry-outpatient-clinic.

There are no psychometric properties yet available for the EPII and optimal scoring procedures are not yet determined. As a covariate in our model, we were only interested in the total cumulative exposure to deleterious events. The total number of deleterious events was normally distributed (skewness = 0.51, SE = 0.17; kurtosis = 0.66, SE = 0.34). This predictor variable (M = 19.39, SD = 7.86) was treated as a continuous variable in all models.

Political Conservatism

The 12-item social and economic conservatism scale (SECS; Everett, 2013) is a measure of political conservatism consisting of two subscales: social conservatism (5 items) and political conservatism (7 items). Higher scores indicate higher levels of conservatism on both scales. The SECS is presented to participants as a continuous scale slider that ranges from 0 (feeling extremely negative toward an issue) to 100 (feeling extremely positive toward an issue). Sample items for social conservatism ($\alpha = 0.86$) include "Abortion" and "Patriotism" and sample items for the economic conservatism subscale (α = 79) include "Limited Government" and "Welfare Benefits." The full SECS is available online: PLOS One doi: 10.1371/journal.pone.0082131.

In this sample, the social (M = 261.15, SD = 180.57) and political (M = 167.81, SD = 112.13) scores were highly correlated (r = 0.64, $p < 0.001$). Both were normally distributed: social conservatism (skewness = 0.09, SE = 0.17; kurtosis = −0.96, SE = 0.34) and political conservatism (skewness = −0.02, SE = 0.17; kurtosis = −0.51, SE = 0.34). Higher scores indicate higher levels of conservatism on both scales. Both scales were modeled individually as exogenous predictor variables to maintain a conceptual distinction.

Demographic Covariates

There were four specific demographic variables that we anticipated having a relationship with our outcome variables: age, sex, religion, and geographic location (see section "Participants").

Specific to geographic location, participants were given the option of reporting their zip code on MTurk; 82.7% of participants (n = 173) provided this information. These zip codes were broken up into geographical regions based on Census demarcation boundaries: Northeast (n = 54), South (n = 46), Midwest (n = 41), Pacific (n = 26), and Mountain (n = 6). We also used this information to find the "% rurality" compiled per county by the most recent census (2010 Census Rural County Lookup)[3]. This produces a continuous variable (0–100) that indicates how "urban" or "rural" a Census-delineated county was as of the last census (higher scores indicating higher rurality). The majority of this sample resided in counties characterized by low rurality (M = 14.31, SD = 18.19). There were no differences on study variables between those who provided zip code information and those who did not (ps > 0.34).

In an attempt to build a parsimonious model (increased df and less model parameters), we explored the bivariate relationship between each of the four demographic variables with the outcome variable in all models. While the decision to exclude variables in models need not only rely on statistical significance, we viewed this step as necessary to eliminate "impotent controls" prior to building a final model (see Becker, 2005) and to limit the number of estimated parameters whenever possible (i.e., Jackson, 2003).

[3]The Census Bureau delineates urban areas after each decennial census. See https://www.census.gov/programs-surveys/geography/guidance/geo-areas/urban-rural.html

Attitudes Toward COVID-19 Precautions

Participants were given a six-point Likert scale anchored with "strongly disagree to strongly agree." Three items were presented to all participants in random order: "How much do you agree with the following statements: (1) Wearing masks in public spaces is necessary; (2) People should continue to stay-at-home (quarantine) even if COVID-19 cases start to fall; (3) The news and threat about COVID-19 is "overblown." A latent outcome variable (named Attitude toward Precautions) was created using all three items on our custom measure. Item loadings ranged from.78 to.86 (all unstandardized estimates $p < 0.001$) which is sufficiently high enough to retain all items as indicators (Hair et al., 1998).

Pandemic Recovery Behavior

Participants were asked the single item "How willing would you be if asked to donate plasma (blood) to helping those with COVID-19?" They responded using an 11-pt scale (0–10) with higher scores indicating more willingness to donate. As a separate item, participants were asked: "How much do you agree with the statement: A vaccine for COVID-19 should be mandatory." Both variables are maintained as continuous outcome variables through all models.

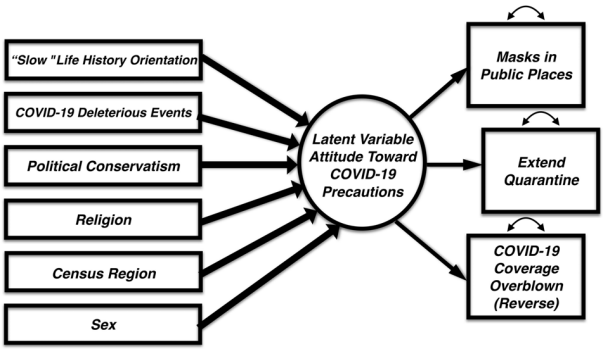

FIGURE 1 | Proposed hybrid structural equation model including all model variables.

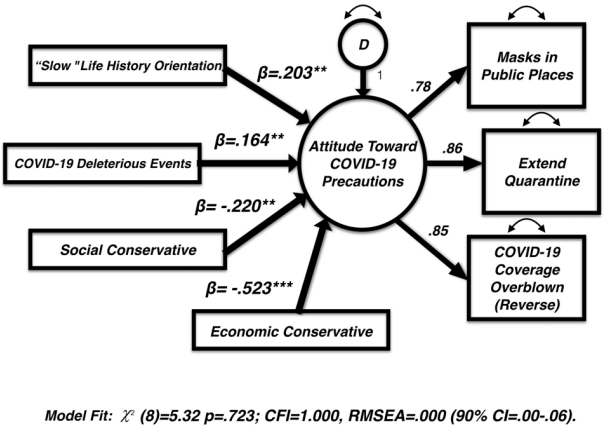

FIGURE 2 | Final hybrid structural equation model including only variables retained. All endogenous (predictor) variables are modeled to covary with one another. Full covariate parameters are found on **Table 1**.

RESULTS

Preliminary Analyses

All analyses were run using SPSS (v. 22) and AMOS (v. 22). Prior to all analyses, variables were examined for normality (skewness, kurtosis, outlier identification). Overall, missingness was minimal with the exception of one item (zip code; see section "Methods") which was elective for participants. We fitted all models using full information maximum likelihood (FIML) estimator using AMOS (v.22). Prior to model building, demographic items (sex, age, region, religion) were explored to identify whether it was appropriate (on statistical grounds) to maintain each in the model building process for each outcome variable examined. A zero order correlation table of all predictor variables is provided on **Supplementary Table 1**. The proposed a prior model can be found in **Figure 1**.

Outcome: Predicting COVID-19 Attitudes Toward Precautions

Demographic Covariates

To examine demographic variables for inclusion in models predicting "Attitudes toward precautions," we ran a series of mean comparisons. Sex ($p = 0.11$), religion ($p = 0.34$), age ($p = 0.30$), and geographical region ($p = 0.12$) were not related to the latent outcome variable. This was also the case when conceptualizing location as the "percentage of rurality" ($p = 0.75$). As a result, we excluded these variables to maintain model parsimony and sufficient degrees of freedom (Achen, 2005).

Model Building and Testing

The resultant model (**Figure 2**) – whereby the latent variable "attitudes toward precautions" is predicted by life history orientation – was tested with the following covariates: social conservatism, economic conservatism, and COVID-19 deleterious events. The tested model fits the data well [$(\chi^2(8) = 5.32, p = 0.723)$; CFI = 1.00, RMSEA = 0.000 (90% CI = 0.000–0.060)]. Life history orientation was able to predict a significant amount of variance in our latent variable "Attitudes Toward Precautions" ($\beta = 0.20, p < 0.01$). Those exhibiting a slow life history orientation were more likely to endorse precautions. This relationship was detectable even after controlling for social and economic conservatism and one's self-reported occurrences of deleterious events resulting from COVID-19. All parameter estimates appear in **Table 1**.

There are other significant relationships in this model that warrant analysis and discussion to a broader audience. In terms of the number of deleterious events, those self-reporting more events were more likely to endorse COVID-19 precautions ($\beta = 0.16, p < 0.01$). There were strong, negative effects for economic ($\beta = -0.52, p < 0.001$) and social conservatism ($\beta = -0.22, p < 0.001$) on the latent variable "Attitudes toward precautions." In both cases, participants who reported being

TABLE 1 | Parameter estimates for modeled predictors of the latent variable Attitudes Toward COVID-19 precautions.

Parameter	Unstd.	SE	Critical ratio	*p*	Std.
Predictor effect					
Slow life history	0.010	0.003	3.136	0.002	0.203
Deleterious events	0.030	0.011	2.791	0.005	0.164
Social conservative (SC)	−0.002	0.001	−2.695	0.007	−0.220
Economic conservative (EC)	−0.007	0.001	−6.591	***	−0.523
Modeled covariance					
Slow life history ↔ SC	2222.865	407.508	5.455	***	0.409
Slow Life History ↔ EC	481.999	236.636	2.037	0.042	0.143
Slow life history ↔ events	54.86	16.858	3.254	0.001	0.232
SC ↔ EC	12902.66	1659.076	7.777	***	0.640
SC ↔ events	128.392	98.355	1.305	0.192	0.091
EC ↔ events	−36.456	60.88	−0.599	0.549	−0.042

*This model fit the data well: [(χ^2(8) = 5.32, p = 0.723); CFI = 1.000, RMSEA = 0.000 (90% CI = 0.00–0.06)]. ***p < 0.001. "SC" = Social Conservatism; "EC" Economic Conservatism; "Events" – deleterious events as a result of COVID-19.*

more conservative were also *less* likely to endorse precautions surrounding COVID-19. Path estimates and covariance values for modeled variables in **Table 1**.

Outcome: Predicting COVID-19 Pandemic Recovery Behavior

Similar testing procedures were used in developing a model that could examine predictors of pandemic recovery behaviors (i.e., plasma donation and vaccine requirements). Each item is tested as an outcome variable separately. The analysis plan will remain consistent: (1) evaluate demographic variables for inclusion in final model; (2) run model to obtain parameter estimates. The analysis for both outcome variables will be equivalent to that of multiple regression with the added benefit of including FIML estimates for missing values (AMOS v22).

Donating Plasma

Sex (p = 0.91), religion (p = 0.78), location (ps > 0.38), and age (p = 0.45) were not related to this "donating plasma" variable and were excluded from models to maintain model parsimony (Achen, 2005). The resultant model – whereby life history orientation predicts one's likelihood to donate plasma – included only the following covariates: social conservatism, economic conservatism, and COVID-19 deleterious events.

In this model, life history orientation was able to predict variance in one's likelihood to donate plasma (β = 0.27, p < 0.001). This relationship was detected after controlling for social and economic conservatism and one's self-reported occurrences of deleterious events resulting from COVID-19. Those exhibiting a slow life history orientation were more likely to report being willing to donate plasma.

In terms of the predictors that accompany life history orientation in this model: those self-reporting more events were more likely to indicate that they would donate plasma (β = 0.19, p < 0.01). Specific to donating plasma, economic conservatism had no relationship to this outcome variable (β = −0.02, p = 0.80). Social conservatism was however related to one's reported likelihood of donating plasma (β = −0.22, p = 0.02) – those higher in social conservatism indicated less interest in donating plasma. Parameter estimates appear on **Table 2**.

COVID-19 Vaccination

Sex (p = 0.54), religion (p = 0.32), location (ps > 0.41), and age (p = 0.52) were not related to this "mandatory vaccination endorsement" variable and were excluded from models to maintain model parsimony (Achen, 2005). As with the model above, all remaining predictors were modeled to covary with one another.

In this model, life history orientation was able to predict variance in one's level of endorsement for the statement "vaccination for COVID-19 should be mandatory" (β = 0.16, p = 0.04). This relationship was detected after controlling for social and economic conservatism and one's self-reported occurrences of deleterious events resulting from COVID-19. Those exhibiting a slow life history orientation were more likely to endorse mandatory vaccination for COVID-19.

In terms of the predictors that accompany life history orientation in this model: those self-reporting more deleterious was not related to one's indication that a vaccination for COVID-19 should be mandatory (β = 0.09, p = 0.13). Specific to the statement "vaccination for COVID-19 should be mandatory," both economic conservatism (β = −0.36, p < 0.001) and social conservatism (β = −0.18, p = 0.04) were negatively

TABLE 2 | Parameter estimates for modeled predictors of (1) Donating Plasma variable and (2) Vaccine variable.

Parameter	Unstd.	SE	Critical ratio	*p*	Std.
1. Predictor effect donate plasma					
Slow life history	0.030	0.008	3.629	***	0.266
Deleterious events	0.080	0.029	2.805	0.005	0.164
Social conservative (SC)	−0.004	0.002	−2.404	0.016	−0.223
Economic conservative (EC)	−0.001	0.003	−0.260	0.765	−0.022
2. Predictor effect mandatory vaccine					
Slow life history	0.012	0.001	−2.067	0.039	0.159
Deleterious events	0.027	0.018	1.502	0.133	0.094
Social conservative (SC)	−0.002	0.001	−2.067	0.039	−0.179
Economic conservative (EC)	−0.007	0.002	−4.463	***	−0.357
Modeled covariance					
Slow life history ↔ SC	2222.865	407.508	5.455	***	0.409
Slow life history ↔ EC	481.999	236.636	2.037	0.042	0.143
Slow life history ↔ events	54.86	16.858	3.254	0.001	0.232
SC ↔ EC	12902.66	1659.076	7.777	***	0.640
SC ↔ events	128.392	98.355	1.305	0.192	0.091
EC ↔ events	−36.456	60.88	−0.599	0.549	−0.042

*"SC" = Social Conservatism; "EC" Economic Conservatism; "Events"-deleterious events as a result of COVID-19; ***p < 0.001. Modeled covariance parameter estimates are identical to latent variable Attitudes Toward COVID-19 precautions.*

correlated with one's level of endorsement for this outcome. Those self-reporting as higher in conservatism were less likely to endorse the statement "A vaccine for COVID-19 should be mandatory." Parameter estimates appear on **Table 2**.

DISCUSSION

In this study, we present evidence that one's life history orientation contributes to which attitudes and behaviors one endorses in the face of an ongoing global pandemic. We utilized three separate outcome variables (attitude toward COVID-19 precautions, willingness to donate plasma, and opinions on COVID-19 vaccination). In each of these models, slow life history strategists adopted a more precautious and prosocial stance (i.e., long term planning). We did not find evidence that sex, age, religiosity, or geographical region ("rurality") had any significant relationship with the outcome variables in this study.

Our results are consistent with extant literature on slow life history strategies and adherence to (and encouragement of) social and moral rules (Gladden et al., 2009). Social and moral rules increase social stability and help maintain a risk-averse environment for one's community. Individuals routinely deploy moral emotions (e.g., anger, disgust) aimed at ensuring the upholding of rules and social contracts (Haidt and Bjorklund, 2008). Interestingly, general disgust sensitivity is thought to have evolved to motivate the avoidance of dangerous pathogens and later coopted to function in a similar manner within the social domain (Navarrete and Fessler, 2006); one can exclude or punish a rule breaker (e.g., refusing to wear a mask) in order to facilitate in-group cohesiveness and to motivate pathogen avoidance. In the context of the current study, slow strategists strongly endorsed more precautious and prosocial behaviors. While we did not measure things like (for example) "disgust toward those not wearing a mask," we expect that, specific to slow life history individuals, one's endorsement of a behavior would be tied to their enforcement of the behavior.

In exploring the contributions of life history orientation, we uncovered relationships that may be of broad interest. In general, political conservatism (social and economic) demonstrated considerable influence on precautionary attitudes and vaccine endorsement; those high in conservatism were lower on endorsement of precautions and vaccines. With regard to plasma donation, economic conservatism (but not social) demonstrated a significant relationship – higher economic conservatism was associated with a lower likelihood of plasma donation. Recent COVID-19 work found that conservatives discount the mainstream media and downplay reports of the severity of the pandemic (Rothgerber et al., 2020). Our work aligns with this research. The decreased levels of endorsement for precautionary measures among conservatives may be a consequence of underestimating risk due to discounting media reports on COVID-19.

One may have predicted that political conservatism to be *positively* correlated with one's level of endorsement of precautions. There is a sizable literature detailing the relationship between conservatism and disgust sensitivity and fear of contamination (see Terrizzi et al., 2013 for a meta-analysis). Pathogen prevalence is positively correlated with authoritarianism (Murray et al., 2013) and conformity (Murray et al., 2011) while negatively correlated with democratic ideals (Thornhill et al., 2009) and openness to experience (Schaller and Murray, 2008). Those high in conservatism should, according to this literature, demonstrate *increased* conformity to precautions. This would also be the same prediction from other research on conservatism that has found a positive relationship with adherence to social norms (e.g., Altemeyer, 1988), avoiding behaviors contrary to a group's best interest (Triandis, 1994), and evidence that socially conservative value systems are partly characterized by submission to authority (see Ludeke et al., 2013).

It is not clear from our data precisely why political conservatism is negatively associated with all three outcome variables in context of extant work. There is some evidence that those who support politically conservative leaders and policies are more likely to believe that the "free market" system is most efficient and to treat this as an ideology of sort (Monteith et al., 2016; Day and Fiske, 2017). A perception of "imposing" on free market forces may be driving down endorsement of precautions, vaccine mandate, and plasma donation. It may also be the case that novel precautions such as wearing a mask or social distancing have yet to reach a critical mass (in the minds of those high in conservatism) as behaviors that are to be conformed to. Even when precautions are socially and/or legally enforced, adherence to these precautions will still rely on cognitive machinery that must identify a behavior as widespread enough where executing that behavior can accurately be tagged as "conforming." Part of the slow strategy itself might be to hold a particularly high threshold for when once novel social behaviors (e.g., wearing a mask) become the norm. While speculative, it may be the case that the COVID-19 pandemic (and all that it brings) offers nuance to the study of conservatism unseen prior. More complex models that include some of these additional variables are needed to address these questions on political conservatism further.

Limitations

Our sample was recruited from the online survey tool MTurk. This sample possessed features that went well beyond what one might find with a standard convenience sample of undergraduates: e.g., age, employment, detrimental pandemic events in a multitude of domains (e.g., work, paying mortgage, quarantine with children, geographical range). MTurk does have limitations however (potential misrepresentation-MacInnis et al., 2020). It is important to note that MTurk participants are typically comparable or better to other data sources (Hauser and Schwarz, 2016; Kees et al., 2017; McCredie and Morey, 2019). Nonetheless, our results may not generalize to the broader population as we did lack representative levels of diversity in terms of race and education. Future research will have to consider MTurk's limitations and benefits.

While the sample size (n = 209) was more than adequate to test our *a priori* models, more complex models

(e.g., mediation, moderation) with many more parameters to estimate would require a much larger sample size than used here. There is potential to convert some of our *a priori* models into *post hoc* mediational models in this dataset. Parameter estimates however would be almost meaningless without an adequate sample size to test those models. This approach is also an effort to avoid what Achen (2005) has called the "kitchen sink" approach to structural equation modeling. Moving and plugging in/out variables, drawing and deleting paths, or finding unjustified (on theoretical grounds) ways to improve model fit are structural equation model strategies that we avoid in this initial attempt.

There is ongoing debate about exactly what is being measured when deploying a measure of life history, specifically with humans (e.g., Stearns and Rodrigues, in press). The life history measure we used here is a psychometric measure of life history orientation that aligns with extant theory and is used widely across research disciplines (Olderbak et al., 2014). Future research should continue to explore the psychometric properties of the life history measure used here. In parallel, debate should proceed in identifying (precisely) which components of theory may apply to humans vs. non-humans.

Future Directions

The COVID-19 pandemic has been accompanied by unprecedented appeals to the greater public for groupwide adherence to precautionary measures and widespread discussion of community-health based medical interventions to "flatten the curve." In this study, we identified the role that life history orientation may play in individual differences related to important decisions around COVID-19 going forward.

These decisions are of great consequence. For example, Hou et al. (2020) found that if the timing of when to declare a quarantine were delayed by even 1.5–2 days, community spread becomes exacerbated. In this context, understanding the predictors of high or low levels of compliance to pandemic precautions or prosocial behaviors is critical. In a study on pandemic influenza, Ekberg et al. (2009) found that a major contributor to reducing disease transmission was the degree to which individuals voluntarily exhibited precautionary behaviors. As some locations re-open across the United States and complacency to precautions increases, the voluntary use of (for example) a mask may become a key contributor to stemming a second wave of the disease.

Pathogens expose vulnerabilities in immunocompetence; pandemics lay bare the workings of cognitive adaptations geared toward negotiating the social environment. Understanding the exact contributions to these types of decisions should pay large dividends on a global scale.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, upon reasonable request.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Institutional Review Board of the University of Massachusetts Boston. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

RC was the Principle Investigator of this study, supervised all activity, wrote the Institutional Review Board (IRB) proposal, evaluated progress on literature review and survey measures, monitored data collection, ran statistical analyses, and drafted this current publication. SD'A, JA, NJ, and KK contributed to hypotheses, to finding applicable measures for this study, to coding the various paper measures for Qualtrics formatting, and to reading over the final publication. SD looked over the IRB proposal, oversaw and contributed to the literature review (specifically compensation and remote data collection method), implemented coding and edits to the Qualtrics survey measures for accuracy and pacing, collected Census data to support analyses, proofread this current publication and wrote this statement. JA, NJ, and KK conducted a comprehensive literature review (for remote recruitment, mechanisms of COVID-19 and prior pandemics, and relation between anxiety and pandemics, respectively), and personally went through the Qualtrics survey multiple times to report on fixable errors. KK and JA also created and organized the Facebook advertisement for the study. All authors contributed to the article and approved the submitted version.

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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.2020.01857/full#supplementary-material

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The Impact of the Covid-19 Pandemic on Disgust Sensitivity

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There have been few tests of whether exposure to naturalistic or experimental disease-threat inductions alter disgust sensitivity, although it has been hypothesized that this should occur as part of disgust's disease avoidance function. In the current study, we asked Macquarie university students to complete measures of disgust sensitivity, perceived vulnerability to disease (PVD), hand hygiene behavior and impulsivity, during Australia's Covid-19 pandemic self-quarantine (lockdown) period, in March/April 2020. These data were then compared to earlier Macquarie university, and other local, and overseas student cohorts, to determine if disgust sensitivity and the other measures, were different in the lockdown sample. The most consistent finding in the lockdown sample was of higher core disgust sensitivity (Cohen's d = 0.4), with some evidence of greater germ aversion on the PVD, and an increase in hand and food-related hygiene, but with little change in impulsivity. The consistency with which greater core disgust sensitivity was observed, suggests exposure to a highly naturalistic disease threat is a plausible cause. Greater disgust sensitivity may have several functional benefits (e.g., hand and food-related hygiene) and may arise implicitly from the threat posed by the Covid-19 pandemic.

Keywords: disgust, infection, avoidance, hand hygiene, germ aversion

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INTRODUCTION

The idea that disgust serves a disease avoidance function has been suggested by several authors and by a number of empirical findings (e.g., Curtis et al., 2004; Oaten et al., 2009). In an examination of potential hypotheses to test the disease avoidance account of this emotion, Oaten et al. (2009) describe in hypothesis 7 how vulnerability to disease should affect disgust, and in particular, how disease threat should result in greater disgust sensitivity. As we outline further below, there have been relatively few tests of this and related hypotheses. Moreover, there have been none using what is probably the most powerful test, namely a naturalistic disease induction (i.e., exposure to a real-world pandemic of infectious disease; Tunnel, 1977; Fernandez-Dols and Civelli, 2013). The aim of the current study is to examine if the Covid-19 pandemic alters participants disgust sensitivity - alongside related measures - by contrasting responses obtained during the pandemic period with responses from comparable previous participant cohorts.

A number of laboratory induction studies have manipulated disease threat by exposing participants to pictures of sick people (e.g., Mortensen et al., 2010; Murray et al., 2013), people sneezing and coughing (Lee et al., 2010), descriptions of migrants who have come from countries believed to harbor more or less infectious disease (Faulkner et al., 2004), and by getting participants to describe a time when they felt especially vulnerable to disease (e.g., Murray and Schaller, 2012).

All of these studies obtained shifts in attitudes, intentions or behaviors, consistent with greater disease avoidance (e.g., reduced extroversion, greater ethnocentricity etc.). These findings indicate that a range of behaviors and dispositions that should aid disease avoidance are increased and so lend indirect support to the idea that other related systems too, such as disgust sensitivity, should also be increased. However, there have been surprisingly few tests of this idea.

One approach has been to see if prior illness might up-regulate disgust sensitivity. Mechanistically, there are at least two ways this might happen. In the first, the biological immune system may act to increase disease avoidant behavior, including disgust. Miller and Maner (2011) tested whether recent illness increased attention to disfigured faces and avoidance of disfigured people and found that it did. They suggest an increase in disease avoidant behavior following illness is not mediated by conscious disease-related knowledge as the effects were independent of current disease concerns (measured using the Perceived Vulnerability to Disease [PVD] questionnaire; Duncan et al., 2009). Two studies using disgust sensitivity have been motivated by this type of approach. Stevenson et al. (2009b) examined the relationship between frequency and recency of common infectious diseases, disgust, and contamination sensitivity. Their results suggested that frequent illness led to heightened contamination sensitivity, which combined with disgust sensitivity, led to fewer illnesses via enhanced behavioral avoidance. However, a further study by de Barra et al. (2014) examining the same hypothesis in a Bangladeshi sample, found no link between disgust sensitivity and illnesses. In addition, Miller and Maner's (2011) findings have also not been replicated (Tybur et al., 2020).

Another approach with the same biological motivation, has been to compare groups of participants who differ in disease risk and see if they also differ in disgust sensitivity. Two studies have adopted this approach. Fessler et al. (2005) examined for heightened disgust sensitivity in the first trimester of pregnancy, when the foetus is most vulnerable to infection. They found heightened disgust sensitivity in the first trimester, consistent with the increased disease risk – but not all studies have replicated this finding either (Jones et al., 2018). Oaten et al. (2017) used a conceptually similar approach, by contrasting people with rheumatoid arthritis who experience more infections (and have higher death rates from them too) with a control sample who did not have this disease. While people with rheumatoid arthritis had highly elevated scores on both subscales of the PVD relative to controls, they did not differ at all in disgust sensitivity, having almost identical means to controls.

Presumably, the circumstances under which we might best expect disgust sensitivity to increase, would be when exposed to a highly salient disease threat. There have been a number of studies that have utilized such naturalistic disease threat inductions, however, they have instead focused on fear of contracting the disease in question, and the predictors of this fear. This approach has been employed for Zika virus (Blakey and Abramowitz, 2017), Ebola (Blakey et al., 2015), and Swine flu (Brand et al., 2013; Wheaton et al., 2012). Interestingly, in each of these studies, contamination sensitivity (in all) and disgust sensitivity (in 3/4) were significant correlates of fear of contracting these various infectious diseases. Relatedly, Fan and Olatunji (2013) also reported that more general health anxiety was significantly related to disgust sensitivity. So, while we do not know if a naturalistic disease induction might affect disgust sensitivity, disgust sensitivity does seem to be implicated in the fear of contracting such diseases and disease fear more generally.

In the current study, our primary focus was on disgust sensitivity. As we wanted to compare our current cohort to previous cohorts that were demographically similar, we used the original 32 item Disgust Scale (DS; Haidt et al., 1994), but only utilized the 27 questions and three sub-scale scores of the revised version of this survey (DS-R; Olatunji et al., 2008, 2009). A further reason for using the DS is that it remains the only self-report disgust sensitivity measure to have been behaviorally validated (Rozin et al., 1999). Two other conceptually related measures were also included. The first was the Hygiene Behavior Inventory, which is a validated and reliable measure to assess multiple aspects of hygiene behavior, including hand washing (Stevenson et al., 2009a,b). This was used because a recent study of people in Croatia undertaken during the Covid-19 self-quarantine (lockdown) period, found large and highly significant increase in safety behaviors, including hand-hygiene (Korajlija and Jokic-Begic, 2020). Logically, we would expect hand-hygiene to increase, and thus to exceed those reported in the past. The second measure was the PVD (Perceived Vulnerability to Disease questionnaire; Duncan et al., 2009). This measure has been widely used to assess perceptions of disease threat and has been used in several related studies (e.g., Oaten et al., 2017). Moreover, much of the reasoning that would suggest that increased disease salience might drive increased disgust sensitivity would also presumably apply to perceived vulnerability to disease. Exactly this prediction was born out in a study that emerged after ours was completed, which found in a United States sample that perceived Covid-19 threat was linked to with higher PVD scores (Makhanova and Shepherd, 2020). The authors also found differences on the two PVD subscales, with the Germ aversion subscale more linked to behavioral disease avoidance and Perceived infectability more linked to disease vigilance. Together, the clear prediction would be of increased PVD scores.

In addition to these main measures, we also collected some other information. First, we included the Barratt Impulsiveness scale (BIS; Spinella, 2007). This was completed as we had no grounds to think that impulsivity would change in response to the Covid-19 pandemic as it is a relatively stable and heritable trait (e.g., Anokhin et al., 2015) and one which is generally negatively correlated with health behaviors (e.g., Duckworth and Kern, 2011). As we had collected BIS data at around the same time as the DS, PVD, and HBI, and in very similar samples, the BIS would serve as a test of any general heightening of response tendencies on survey instruments. Second, we also obtained basic demographic information, namely age and gender, as both are known to moderate disgust sensitivity (e.g., Haidt et al., 1994; Druschel and Sherman, 1999; Al-Shawaf et al., 2018). Participants were also asked whether they were ill now, whether they had been recently ill, and their general health status, on the basis that these variables might also modify responding (e.g., Prokop et al., 2010). The survey was undertaken during Australia's lockdown

period, and the studies relationship to the timeline of events is presented in **Table 1**. The date on which participants completed the survey was also used as a variable, on the basis that the further into the lockdown period the survey was completed, the more intense and saturated (i.e., media coverage, large change in routines of work, study and socialization, etc.) were peoples experience of the pandemic.

MATERIALS AND METHODS

Participants

Three-hundred and twenty-two Macquarie University undergraduate psychology students started the survey and 310 successfully completed it for course credit. The survey was open from 23rd April 2020 and closed on the 30th May 2020. The survey opening date was around 3 months after the Covid-19 pandemic started to dominate news media in Australia (see **Table 1** for timeline) and data was collected during the most intense phase of the pandemic, with Australia in lockdown for the study period. We refer to this sample as MU20 (i.e., data collected at Macquarie University in 2020).

The study protocol was approved by Macquarie University human ethics committee. Participants were informed at the start of the survey that the aim was to study relationship between emotion and behavior, and that they would be completing various questionnaires relating to disgust, perceptions of threat, hygiene and impulsivity – wording of the aim was vague and based on prior information statements used in collecting these sorts of data at Macquarie University. Participants were informed that completion of the survey indicated consent to use their data. At the end of the survey, participants were presented with a written debrief about the study's primary aim and they were asked not to disclose this to other students.

Comparison Samples

Seven comparison samples were used to establish if the MU20 sample might report alterations in the various study measures. Four of the comparison samples were collected at Macquarie University, one during 2008, one during 2009, one during 2010 and one during 2014. All four were completed wholly or mainly (more below) on first year psychology students using on-line data collection with Qualtrics. We detail each sample in turn.

The 2008 Macquarie sample (MU08), formed Study 5 of Stevenson et al. (2009a,b). Study 5 was composed primarily of first-year undergraduates, alongside participants from the university and local community. These participants completed online, the Hygiene Behavior Inventory (HBI), the Disgust Scale (original 32 item version), the Perceived Vulnerability to Disease questionnaire, alongside other measures (Mini-marker, Padua contamination index). The aim of the study was to test the construct validity of the HBI.

The 2009 Macquarie sample (MU09), is from an unpublished survey undertaken by author TIC, exploring contamination beliefs using the vignette based Rozin 'sweater task' (i.e., would you wear a sweater who had been worn by. . .). First-year undergraduates completed the Rozin 'sweater task' and then the PVD and the Disgust Scale (original 32 item version), as part of their course requirements.

TABLE 1 | Covid-19 timeline in Australia, prior to and during the survey period.

Date	Event
25/1/20	First Australian Covid-19 infection identified; China travel alert issued
3/2/20	Australians evacuated from Wuhan to quarantine on Christmas island
5/2/20	Mandatory quarantine for arrivals from China
11/2/20	13 cases now identified
1/3/20	First Covid-19 death
3/3/20	Panic buying starts in supermarkets
7/3/20	73 cases identified, 2 deaths
11/3/20	WHO declares global pandemic
15/3/20	298 cases identified, 5 deaths; Ban on gatherings of 500+ people
16/3/20	Macquarie University stops face-to-face teaching; Foreign arrivals must self-isolate; Shopping limits imposed at supermarkets
17/3/20	All international travel banned
18/3/20	Ban on gatherings of 100+
20/3/20	875 cases identified, 7 deaths; Social distancing rules enacted
23/3/20	Lock-down starts; Macquarie University campus closed; Schools, all entertainment venues, gyms, sports venues, many shops closed
25/3/20	2432 cases identified, 9 deaths; State borders closed
29/3/20	All Australians instructed to stay home unless in vital employment
1/4/20	4864 cases identified, 21 deaths
23/4/20	**Survey starts**; 6661 cases identified, 75 deaths
30/4/20	6762 cases identified, 92 deaths
2/5/20	Large out-break in Victoria
15/5/20	First easing of restrictions in NSW, with up to 10 patrons in restaurants
30/5/20	**Survey ends**

The 2010 Macquarie sample (MU10), was also an unpublished survey undertaken by TIC, to explore a vignette-based measure of contamination, using product choices by stigma targets to see if this would affect hypothetical purchase decisions. First-year undergraduates completed this task and then the PVD and the Disgust Scale (original 32 item version), as part of their course requirements.

The 2014 Macquarie sample (MU14), formed the sample for Study 1 of Lumley et al., 2016, exploring the relationship between diet and impulsivity. Participants completed online the short form Barratt Impulsiveness Scale (BIS), a brief food frequency measure and demographic variables.

The 2009 University of Western Australia (UWA09) comparison, which consisted of just means and SDs for the Disgust Scale (original 32 item version), gender distribution and age, was obtained from **Tables 1**, **2** from Olatunji et al. (2009). This study reports samples from 8 different countries as part of a validation of the revised DS. We selected the Australian sub-study to provide a further Australian student sample from another university.

The 2008 Fordham University (USA08) comparison, again consisting of means and SDs for the Disgust Scale (original 32 item version), gender distribution and age, was obtained from Olatunji et al. (2008). Olatunji et al. (2008) report four studies in total aimed at developing and validating a revision of the DS, and we selected just the Fordham sample (Study 3) as it was the largest and most comparable in gender distribution.

The 2009 University of British Columbia (UBC09) comparison, consisted of means and SDs for the PVD, gender distribution and age, reported as part of the development and validation of this scale (Duncan et al., 2009). A smaller Dutch sample was also included, but we selected the larger UBC sample both because of its size and due to the greater cultural and linguistic similarity between Canada and Australia.

Measures

The Disgust Scale (DS) was administered in its original 32-item version (Haidt et al., 1994), to provide the same question context as the various comparison samples described above. We then used the subset of 25 items identified in Olatunji et al.'s (2008) revision (DS-R), and its three resultant subscales (Core, Animal reminder, Contamination), alongside the total score. The DS-R has good overall reliability (alpha > 0.8), with adequate reliability for the subscales.

The Perceived Vulnerability to Disease (PVD) questionnaire is a 15-item measure assessing participants perceived susceptibility to catching disease and their aversion to pathogens. The scale has good reliability, as do each of its two subscales (Germ aversion and Perceived infectability; alpha > 0.74).

The Hygiene Behavior Inventory (HBI) is a 23-item measure that asks participants about several domains of hygiene-related behavior (Stevenson et al., 2009a,b). The scale has 5 subscales, measuring General hygiene (8 items, 6 on hand washing situations), Household hygiene (3 items on household cleaning), Food-related hygiene (3 items on preparing food), Hand hygiene technique (5 items on knowledge about appropriate means of washing hands) and Personal hygiene (4 items on clothing change and bathing habits). Overall reliability for the scale is good (alpha = 0.85), and subscale alphas range from good to adequate (0.82–0.67). Responses on the HBI predict hand hygiene behavior and reported infection rates for common illnesses (Stevenson et al., 2009a,b).

The short form Barratt Impulsiveness scale (BIS) is a 15-item measure that assesses impulsivity (Spinella, 2007). The scale has

TABLE 2 | Correlation (Pearson's) between the main measure totals and scale scores (5% critical alpha = ± 0.11) for the current dataset.

Scales	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.
Subscales																
1. DS-R Total$_1$	0.86	0.80	0.67	0.49	0.58	0.18	0.50	0.47	0.22	0.34	0.35	0.17	−0.06	−0.01	−0.11	−0.01
2. Core		0.47	0.44	0.44	0.52	0.16	0.47	0.42	0.24	0.29	0.34	0.18	0.05	−0.01	−0.13	−0.01
3. Animal			0.35	0.31	0.34	0.15	0.27	0.26	0.09	0.26	0.19	0.05	0.04	0.04	−0.01	0.06
4. Contamination				0.42	0.54	0.10	0.48	0.50	0.20	0.24	0.32	0.18	−0.17	−0.13	−0.15	−0.12
5. PVD Total$_2$					0.82	0.76	0.51	0.49	0.24	0.24	0.44	0.14	−0.09	−0.09	−0.12	−0.02
6. Germ aversion						0.28	0.62	0.61	0.25	0.30	0.48	0.21	−0.21	−0.18	−0.21	−0.10
7. Perceived infectability							0.17	0.15	0.12	0.07	0.20	−0.00	0.07	0.05	0.03	0.08
8. HBI Total$_3$								0.88	0.51	0.56	0.74	0.45	−0.24	−0.17	−0.24	−0.15
9. General hygiene									0.27	0.42	0.57	0.21	−0.19	−0.16	−0.17	−0.12
10. Household hygiene										0.21	0.32	0.15	−0.20	−0.12	−0.23	−0.12
11. Food-related hygiene											0.28	0.08	−0.09	−0.02	−0.10	−0.08
12. Hand hygiene technique												0.15	−0.18	−0.10	−0.25	−0.06
13. Personal hygiene													−0.12	−0.09	−0.08	−0.12
14. BIS Total$_4$														0.81	0.71	0.82
15. Motor															0.32	0.56
16. Non-planning																0.37
17. Attention																

$_1$ Disgust Scale-Revised. $_2$ Perceived Vulnerability to Disease. $_3$ Hygiene Behavior Inventory. $_4$ Barratt Impulsiveness Scale.

three sub-scales (Motor, Non-planning and Attention), with good overall reliability (alpha > 0.79; sub-scale alphas not reported).

Procedure

Participants completed the online Qualtrics survey in a fixed order, undertaking the DS-R, then the PVD, HBI and the BIS. The date the survey was completed was also recorded. After completing the questionnaires, participants were asked to report their age and gender, their current health [five point category scale from 1 (Poor) to 5 (Excellent)], and whether they had been ill in the last month, week or were currently ill (in each case Yes, No, Unsure). Six check questions were randomly interspersed throughout the survey to ensure that participants were paying attention and not answering in a repetitive manner. All of these were correctly answered by the participants. A brief one paragraph debriefing was presented on completion of the survey.

Analysis

Apart from illness recency and general health, the remaining data were normally distributed and suitable for parametric testing. Bivariate relationships were established using Pearson's for normal data, with Spearman's for correlations involving non-normal variables. To check differences between samples in age and gender distribution, independent *t*-tests were used for the former and chi-squared for the latter. Two main analysis approaches were then used. The first, where we had access to raw data, used Multivariate Analysis of Covariance (MANCOVA), with Sample (MU20 vs. comparison) and Gender as between subject factors, sub-scale scores as the dependent variables and age as the covariate. Both the outcome of the multivariate tests (i.e., Sample, Gender, Gender by Sample) and the univariate effects for each sub-scale are reported. The second approach was employed for comparisons where we only had access to means and standard deviations. Here we used independent t-tests on each sub-scale score.

RESULTS

Analysis of Just the MU20 Sample

Correlations between the measures for the MU20 sample obtained during the Covid-19 lockdown are detailed in **Table 2**. Consistent with the previous literature, greater disgust sensitivity (DS-R) was positively associated with greater perceived vulnerability to disease (PVD), and especially so for its germ aversion subscale. Greater disgust sensitivity and greater perceived vulnerability to disease were both correlated with greater self-reported propensity for hygiene behaviors (HBI). Better self-reported hygiene, greater disgust sensitivity and greater perceived vulnerability to disease were all weakly linked to lower levels of self-reported impulsivity (BIS).

The MU20 sample were asked about their current general health status, with the modal response being good (48.1%). MU20 participants were also asked about recent illness, with 21.6% reporting having been ill in the last month, 9.4% in the last week and 5.5% while completing the survey. We also recorded when during the data collection period the survey was completed – testing order. All of these variables were then correlated (Spearman's rho) with the total scores of the main measures, partialling out age and gender. The correlations are presented in **Table 3**. The recent illness variables were unrelated to any of the main measures. However, better general health was linked to both lower reported perceived vulnerability to disease (PVD) and to less impulsive behavior (BIS).

The later participants completed the survey (i.e., the further into the lockdown period of the pandemic) the higher their scores on both disgust sensitivity (DS-R) and on the PVD. For the DS-R, the mean score for participants who completed data collection in the first half of the survey collection period was 14.5 (SD = 4.2), increasing to a mean of 15.6 (SD = 4.1) in the second half of the survey collection period – a 4.4% increase. For the PVD, the comparable change in means was from 3.7 (SD = 0.9) to 3.9 (SD = 0.8), representing a 2.9% increase.

Comparison of the MU20 Sample to Other Student Samples for Disgust Sensitivity

Descriptive data for the MU20 sample and the comparison samples for disgust sensitivity are presented in **Table 4**. Five comparison samples were available, three from Macquarie (MU10, 09, 08), one from the University of Western Australia (UWA09) and one from Fordham University (USA08) in the United States. The MU20 sample was significantly younger - by around 1 year - than the other Macquarie samples ($p < 0.016$), hence our use of age as a covariate in the analyses using raw data

TABLE 3 | Correlation (Spearman) between testing order, general health, and recent illness, and the total scores for the main measures, partialling out age and gender, for the current dataset.

Variable	Testing order	General health	Unwell past month	Unwell past week	Unwell now
$DS\text{-}R_1$	0.14*	−0.05	0.02	0.10	0.02
PVD_2	0.12*	−0.18*	−0.06	−0.06	−0.03
HBI_3	0.03	0.07	−0.02	−0.01	0.05
BIS_4	0.06	−0.23*	0.03	0.00	−0.02

*$p < 0.05$. $_1$ *Disgust Scale-Revised.* $_2$ *Perceived Vulnerability to Disease.* $_3$ *Hygiene Behavior Inventory.* $_4$ *Barratt Impulsiveness Scale.*

TABLE 4 | Sample details for the analyses of the Disgust Scale-Revised (DS-R).

Study (Name)	*n* =	Mean	DS-R subscales means (SDs)		
Year	(%female)	Age (SD)	Core	Animal	Contamination
Macquarie university students during CV19 lockdown (MU20)					
2020_1	310 (75.2)	19.8 (3.8)	8.19 (2.14)	5.01 (1.94)	1.85 (1.19)
Macquarie university students in previous years (MU10, 09 and 08)					
2010_2	467 (68.7)	20.8 (5.3)	7.40 (2.39)	4.86 (1.66)	1.83 (1.19)
2009_3	632 (73.7)	20.6 (5.2)	7.30 (2.43)	4.98 (1.68)	1.69 (1.16)
2008_4	507 (74.6)	21.0 (5.2)	7.40 (2.37)	4.11 (1.80)	1.78 (1.19)
Australian (non-Macquarie) university students in previous years (UWA09)					
2009_5	646 (71.5)	18.9 (4.5)	6.60 (2.28)	3.92 (2.00)	0.95 (0.95)
American university students in previous years (USA08)					
2008_6	363 (74.0)	20.0 (1.6)	7.32 (2.64)	5.36 (2.08)	3.55 (1.45)

$_1$ Macquarie university psychology undergraduate sample collected during the Covid-19 lockdown and university closure period. $_2$ Macquarie university psychology undergraduate sample collected in 2010 by author TIC. $_3$ Macquarie university psychology undergraduate sample collected in 2009 by author TIC. $_4$ Macquarie university psychology undergraduate sample collected as part of the American Journal of Infection Control study published by RS and TC. $_5$ Australian arm (UWA: University of Western Australia) of Olatunji et al., 2009. $_6$ Study 3 Olatunji et al., 2008, collected from undergraduates at Fordham university, New York.

TABLE 5 | Comparison of the current sample with previous student samples for the Disgust Scale-Revised.

Comparison						
Statistical methods and outcomes						
MANCOVA (age as covariate)	**Sample (S)**	**Gender (G)**	**Gender × Sample (G × E)**	**Univariate effects for Sample for Core (C)**	**Univariate effects for Sample for Animal (A)**	**Univariate effects for Sample for Contamination (N)**
MU20 vs. MU10						
	S: $F_{3,770} = 6.60$*, $\eta^2 = 0.03$	G: $F_{3,770} = 53.95$*, $\eta^2 = 0.17$	G × S: $F_{3,770} = 0.17$, $\eta^2 = 0.00$	C: $F_{1,772} = 12.97$*, $\eta^2 = 0.02$	A: $F_{1,772} = 0.04$, $\eta^2 = 0.00$	N: $F_{1,772} = 0.07$, $\eta^2 = 0.00$
MU20 vs. MU09						
	S: $F_{3,935} = 12.15$*, $\eta^2 = 0.04$	G: $F_{3,935} = 57.87$*, $\eta^2 = 0.16$	G × S: $F_{3,935} = 0.39$, $\eta^2 = 0.00$	C: $F_{1,937} = 27.20$*, $\eta^2 = 0.03$	A: $F_{1,937} = 0.12$, $\eta^2 = 0.00$	N: $F_{1,937} = 2.32$, $\eta^2 = 0.00$
MU20 vs. MU08						
	S: $F_{3,810} = 12.71$*, $\eta^2 = 0.05$	G: $F_{3,810} = 56.34$*, $\eta^2 = 0.17$	G × S**: $F_{3,810} = 4.30$*, $\eta^2 = 0.02$	C: $F_{1,812} = 25.01$*, $\eta^2 = 0.03$	A: $F_{1,812} = 27.68$*, $\eta^2 = 0.03$	N: $F_{1,812} = 4.96$*, $\eta^2 = 0.01$
	Independent *t*-tests (only Ms and SDs available)					
	Core (C)	**Animal (A)**	**Contamination (N)**			
MU20 vs. UWA09						
	C: $t_{954} = 10.29$*, $r^2 = 0.10$	A: $t_{954} = 7.96$*, $r^2 = 0.06$	N: $t_{954} = 12.59$*, $r^2 = 0.14$			
MU20 vs. USA08						
	C: $t_{671} = 4.64$*, $r^2 = 0.03$	A: $t_{671} = -2.24$*, $r^2 = 0.01$	N: $t_{671} = -16.45$*, $r^2 = 0.29$			

*$p < 0.05$. **Univariate effects revealed that the Gender x Sample interaction was only significant for N, $F_{1,812} = 9.02$*, $\eta^2 = 0.01$.*

(i.e., MU10, 09, 08). The UWA09 sample was also significantly younger than the MU20 sample by a similar amount ($p = 0.0009$) but the USA08 sample did not differ in age. As we did not have raw data for these last two comparisons, age difference could not be corrected for the UWA09 sample. For the proportion of males to females, only the MU10 sample differed from the MU20 ($p = 0.044$; all other p's > 0.21), but as gender could potentially moderate some of the psychological effects of Covid-19 pandemic, it was included as an independent variable in the analyses using raw data (i.e., MU10, 09, 08).

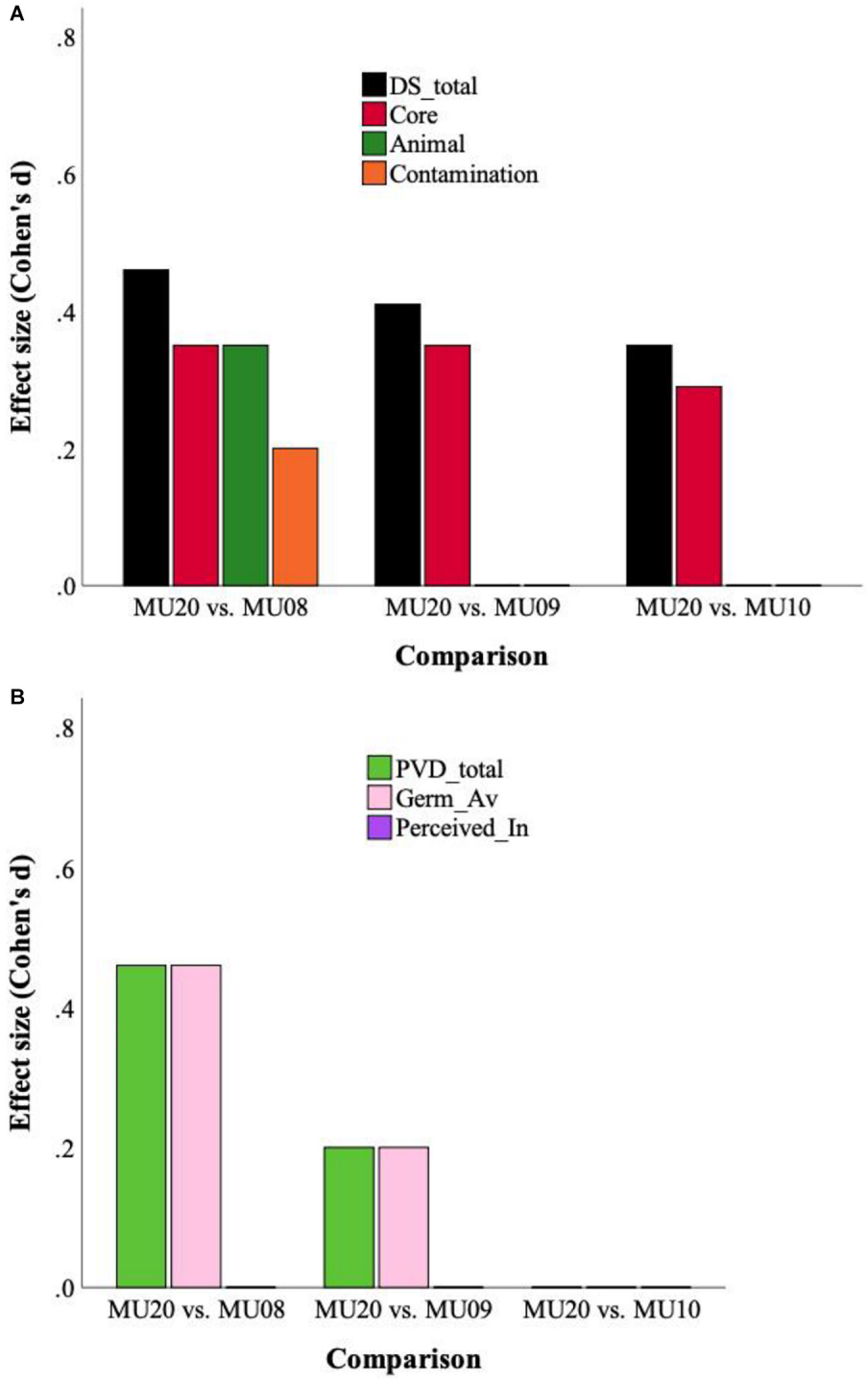

FIGURE 1 | (A) Effect sizes for Disgust Sensitivity (DS) total score and subscales, for the three raw data analyses. **(B)** Effect sizes for Perceived Vulnerability to Disease (PVD) and subscales (Germ aversion, Perceived infectability), for the three raw data analyses.

The two different sets of analyses are presented in **Table 5**. The raw data analyses, using MANCOVA (Sample, Gender; Age as covariate) with the three subscales as dependent variables, revealed significant effects of Sample and of Gender, for each of the three analyses, with an interaction between Sample and Gender for just the MU08 comparison [here the gender difference for Contamination was larger in the MU08 sample (M = 0.9), than in the

MU20 sample (M = 0.4)]. In all three analyses, disgust sensitivity was higher in the MU20 sample, and as would be expected, higher in women across all samples. Univariate effects for Sample are also reported in **Table 5**. Only Core disgust was significantly higher in all three comparisons. The raw data analyses are illustrated using effect size in **Figure 1A**.

The two final samples, UWA09 and USA08 were analyzed by independent t-tests, one for each subscale (see **Table 5**). For the UWA09 comparison, Core, Animal reminder and Contamination disgust sensitivity were higher in the MU20 sample. For the USA08 comparison, Core disgust was greater in the MU20 sample, but the Fordham students reported significantly higher Animal reminder and Contamination disgust sensitivity. In sum, the consistent finding from this set of analyses was of higher reported core disgust sensitivity in the MU20 sample.

Comparison of the MU20 Sample to Other Student Samples for Perceived Vulnerability to Disease

Relevant descriptive data for the MU20 sample and the comparison samples for the PVD questionnaire are presented in **Table 6**. Four comparison samples were available, three from Macquarie (MU10, 09, 08), and one from Canada (UBC09). As noted, the MU20 sample was significantly younger - by around 1 year - than the three Macquarie samples (an age comparison could not be made for the UBC sample, but it too is around 1 year older than the MU20 sample). The MU10 sample also had slightly but significantly fewer women and more men than the MU20 sample. There were no differences in gender distribution for the other comparison samples.

Two sets of analyses were completed, which are presented in **Table 7**. The first used MANCOVA, and revealed significant effects of Gender in all cases, no Sample by Gender interactions, and effects of Sample for two out of the three comparisons. PVD scores were higher overall for the MU20 sample in the MU09 and MU08 comparisons. Females consistently scored higher than males. Univariate effects for sample are also reported in **Table 7**. There were no univariate effects for the MU10 comparison, but for MU09 and MU08, the Germ Aversion subscale, but not the Perceived Infectability subscale, was higher in the MU20 sample. The raw data analyses are illustrated using effect size in **Figure 1B**.

The final comparison used independent t-tests, one for each subscale (see **Table 7**). Relative to UBC09, the MU20 sample had a higher overall PVD score, and a higher Germ Aversion subscale score. There was no difference for the perceived infectability subscale. These analyses provide some evidence of an increase in germ aversion in the MU20 sample, noting that this subscale is far more strongly correlated with core disgust sensitivity than perceived infectability (see **Table 2**; Williams test comparison, $p < 0.001$).

TABLE 6 | Sample details for the analyses of the Perceived Vulnerability to Disease (PVD) Questionnaire.

Questionnaire					
Study (Name)	**n =**	**Mean**	**PVD – Means (SDs)**		
Year	**(%female)**	**Age (SD)**	**Total score**	**Germ Aversion**	**Perceived infectability**
Macquarie university students during CV19 lockdown (MU20)					
2020_1	310 (75.2)	19.8 (3.8)	3.83 (0.83)	4.03 (1.02)	3.59 (1.06)
Macquarie university students in previous years (MU10, 09, and 08)					
2010_2	467 (68.7)	20.8 (5.3)	3.75 (0.93)	3.88 (1.09)	3.61 (1.30)
2009_3	632 (73.7)	20.6 (5.2)	3.73 (0.89)	3.81 (1.02)	3.63 (1.27)
2008_4	507 (74.6)	21.0 (5.2)	3.49 (0.90)	3.44 (1.03)	3.56 (1.30)
Canadian university students in previous years (UBC09)					
2009_5	1332 (75.6)	20.8_5	3.67 (1.07)	3.81 (1.02)	3.52 (1.12)

$_1$ Macquarie university psychology undergraduate sample collected during the Covid-19 lockdown and university closure period. $_2$ Macquarie university psychology undergraduate sample collected in 2010 by author TIC. $_3$ Macquarie university psychology undergraduate sample collected in 2009 by author TIC. $_4$ Macquarie university psychology undergraduate sample collected as part of the American Journal of Infection Control study published by RS and TC. $_5$ Canadian university students at the University of British Columbia reported in Duncan et al., 2009. $_5$ No SD provided.

Comparison of the MU20 Sample to Another Student Sample for Hygiene Behavior

Relevant descriptive data for the MU20 sample and the comparison sample for the HBI questionnaire is presented in **Table 8**. The comparison sample was significantly older (by around 1 year), but with no difference in gender distribution.

The analyses are presented in **Table 9**. MANCOVA revealed significant effects of Sample and Gender, and a Sample by Gender interaction [here the gender difference for General hygiene was larger in the MU20 sample (M = 0.4), than for the MU08 sample (M = 0.1)]. Overall, self-reported hygiene scores were higher in the MU20 sample, and in women in both samples. Univariate effects for Sample are also reported in **Table 9**. Significant effects on three subscales were evident, General hygiene, Food-related hygiene and Hand-hygiene technique.

Comparison of the MU20 Sample to Another Student Sample for Impulsivity

Relevant descriptive data for the MU20 sample and the comparison sample for the BIS questionnaire is presented in **Table 10**. The MU14 comparison sample was the same age ($p = 1$) but had significantly more men than the MU20 sample ($p < 0.01$). The analyses are presented in **Table 11**. MANCOVA (Sample, Gender; Age as covariate), with the three subscales of the BIS as dependent variables, revealed only a significant effect of Gender, with women reporting slightly lower levels of impulsivity than men. Univariate effects for Sample are also reported in **Table 11**. A small univariate effect was present for the Attention subscale –

TABLE 7 | Comparison of the current sample with previous student samples for the Perceived Vulnerability to Disease Questionnaire.

Comparison					
	Statistical methods and outcomes				
MANCOVA (age as covariate)	**Sample (S)**	**Gender (G)**	**Gender × Sample (G × E)**	**Univariate effects for Sample for Germ aversion (GA)**	**Univariate effects for Sample for Infectability (PI)**
MU20 vs. MU10	S: $F_{2,771} = 1.10$, $\eta^2 = 0.00$	G: $F_{2,771} = 18.19$*, $\eta^2 = 0.05$	G **x** S: $F_{2,771} = 0.08$, $\eta^2 = 0.00$	GA: $F_{1,772} = 1.28$, $\eta^2 = 0.00$	PI: $F_{1,772} = 0.49$, $\eta^2 = 0.00$
MU20 vs. MU09	S: $F_{2,936} = 3.54$*, $\eta^2 = 0.01$	G: $F_{2,936} = 25.84$*, $\eta^2 = 0.05$	G × S: $F_{2,936} = 1.13$, $\eta^2 = 0.00$	GA: $F_{1,937} = 6.64$*, $\eta^2 = 0.01$	PI: $F_{1,937} = 0.01$, $\eta^2 = 0.00$
MU20 vs. MU08	S: $F_{2,811} = 21.84$*, $\eta^2 = 0.05$	G: $F_{2,811} = 17.69$*, $\eta^2 = 0.04$	G × S: $F_{2,811} = 0.97$, $\eta^2 = 0.00$	GA: $F_{1,812} = 42.61$*, $\eta^2 = 0.05$	PI: $F_{1,812} = 0.11$, $\eta^2 = 0.00$
Independent t-tests (only Ms and SDs available)					
	Total (T)		**Germ (GA),**		**Infectability (PI)**
MU20 vs. UBC09	T: $t_{1640} = 2.47$*, $r^2 = 0.00$		GA: $t_{1640} = 3.42$*, $r^2 = 0.01$		PI: $t_{1640} = 1.00$, $r^2 = 0.00$

*$p < 0.05$.

TABLE 8 | Sample details for the analyses of the Hygiene Behavior Inventory.

Study (Name) Year	***n* =**	**Mean**	**Hygiene Behavior Inventory – Means (SDs)**					
	(%female)	**Age (SD)**	**Total score**	**General hygiene**	**Household hygiene**	**Food-related hygiene**	**Hand-hygiene technique**	**Personal hygiene**
Macquarie university students during CV19 lockdown (MU20)								
2020_1	310 (75.2)	19.8 (3.8)	3.13 (0.37)	3.02 (0.57)	3.50 (0.56)	3.62 (0.54)	2.94 (0.45)	2.97 (0.53)
Macquarie university students in previous years (MU08)								
2008_2	507 (74.6)	21.0 (5.2)	2.92 (0.38)	2.78 (0.52)	3.48 (0.61)	3.26 (0.71)	2.56 (0.53)	3.02 (0.54)

$_1$ Macquarie university psychology undergraduate sample collected during the Covid-19 lockdown and university closure period. $_2$ Macquarie university psychology undergraduate sample collected as part of the American Journal of Infection Control study published by RS and TC.

TABLE 9 | Comparison of the current sample with previous student sample for the Hygiene Behavior Inventory.

Comparison	Statistical method and outcome								
MANCOVA (age as covariate)	**Sample (S)**	**Gender (G)**	**Gender × Sample (G × E)**	**Univariate effects for Sample for General hygiene (GH)**	**Univariate effects for Sample for Household hygiene (HH)**	**Univariate effects for Sample for Food-related hygiene (FRH)**	**Univariate effects for Sample for Hand-hygiene technique (HHT)**	**Univariate effects for Sample for Personal hygiene (PH)**
MU20 vs. MU08	S: $F_{5,808} = 21.47^*$, $\eta^2 = 0.12$	G: $F_{5,808} = 12.84^*$, $\eta^2 = 0.07$	G × S**: $F_{5,808} = 2.67^*$, $\eta^2 = 0.02$	GH: $F_{1,812} = 15.99^*$, $^2 = 0.02$	HH: $F_{1,812} = 0.00$, $\eta^2 = 0.00$	FRH: $F_{1,812} = 36.97^*$, $\eta^2 = 0.04$	HHT: $F_{1,812} = 77.27^*$, $\eta^2 = 0.09$	PH: $F_{1,812} = 0.09$, $\eta^2 = 0.00$

*$p < 0.05$. **Univariate effects revealed that the Gender x Sample interaction was only significant for GH, $F_{1,812} = 6.83^*$, $\eta^2 = 0.01$.

this being reportedly poorer in the MU20 sample, but no effects on the Motor or Non-planning subscales were evident.

DISCUSSION

The MU20 sample who completed the disgust sensitivity measure and other scales during Australia's lockdown period of the Covid-19 pandemic, reported overall higher levels of disgust sensitivity than the Macquarie university comparison samples. When looking at the three subscales that constitute the DS-R, core disgust was consistently elevated (M Cohen's $d = 0.4$), both in the three Macquarie university comparison samples and also relative to those of students from another Australian university and from an American university. There was no evidence that the presumed Covid-19 effect on core disgust was moderated by gender, although gender moderation was observed in one comparison, and then only for the contamination subscale. There was also some evidence that one of the two PVD subscales was elevated in the MU20 sample. While no changes were observed for the perceived infectability subscale, germ aversion was higher in the MU20 sample in 3 of the 4 comparisons (M Cohen's $d = 0.2$). As would be expected, participants in the MU20 sample reported higher scores for hygiene behavior overall (Cohen's $d = 0.7$), and on the subscales for hand-hygiene technique, general hygiene (6/8 items on hand washing occasions) and food-related hygiene. This is consistent with another Covid-19 study, which also found significant increases in safety behaviors, which included hand washing (Korajlija and Jokic-Begic, 2020). We also examined for changes in impulsivity, finding no overall effect, except for a single small univariate effect on the attention subscale (Cohen's $d = 0.2$; poorer attention in the MU20 sample).

A significant concern in comparing data from one cohort to another, is whether any differences between the two arose from reasons other than the variable of interest (i.e., Covid-19). While no definitive answer to this concern can be given, there are several reasons to regard the observed differences as arising primarily from the Covid-19 pandemic. First, both authors RS and TC have worked at Macquarie University for the whole of the time period covered by the analyses. We are not aware of any major changes in demographics or sources of students into the university over the time periods covered here. Second, it is important to also identify the variables that were not reliably different when the samples were compared, especially given the power here to detect even small differences. The perceived infectability subscale of the PVD remained consistently similar, perhaps reflecting this measures sensitivity to personal infection history (i.e., the items pertain to belief that one will fall ill) rather than to perceptions of infection risk (e.g., Oaten et al., 2017). On the hygiene inventory (HBI), personal and household hygiene scores also remained stable. These subscales have no hand hygiene components, refer to frequency of clothing change and room cleaning, which might be expected to be least affected by a disease-related upswing in hygiene behavior. Reported impulsivity was also very similar, differing unexpectedly in only one subscale, with a small effect size. Third, the pattern of gender differences for all of the variables remained largely consistent across the cohorts,

TABLE 10 | Sample details for the analyses of the short form Barratt Impulsiveness Scale (BIS).

Study (Name)						
Year	***n*** **= (%female)**	**Mean Age (SD)**	**BIS – Means (SDs)**			
			Total score	**Motor**	**Non-planning**	**Attention**
Macquarie university students during CV19 lockdown (MU20)						
2020_1	310 (75.2)	19.8 (3.8)	33.20 (6.76)	10.95 (2.94)	10.95 (2.81)	11.31 (2.88)
Macquarie university students in previous years (MU14)						
2014_2	571 (66.7)	19.8 (4.6)	32.57 (6.76)	11.00 (2.97)	10.75 (2.96)	10.82 (2.97)

$_1$ Macquarie university psychology undergraduate sample collected during the Covid-19 lockdown and university closure period. $_2$ Macquarie university psychology undergraduate sample (MU14) collected as part of the Personality and Individual Differences study published by RS.

TABLE 11 | Comparison of the current sample with a previous student sample for the short form Barratt Impulsiveness Scale (BIS).

Comparison						
	Statistical method and outcomes					
MANCOVA (age as covariate),	**Sample (S),**	**Gender (G)**	**Gender × Sample (G × E)**	**Univariate effects for Sample for Motor (M)**	**Univariate effects for Sample for Non-planning (NP)**	**Univariate effects for Sample for Attention (A)**
MU20 vs. MU14						
	S: $F_{3,874}$= 2.59, η^2 = 0.01	G: $F_{3,874}$ = 3.76*, η^2 = 0.01	G **x** S: $F_{3,874}$ = 0.04, η^2 = 0.00	M: $F_{1,876}$ = 0.02, η^2 = 0.00	NP: $F_{1,876}$ = 1.54, η^2 = 0.00	A: $F_{1,876}$ = 4.20*, η^2 = 0.01

*$p < 0.05$.

suggesting stability in this regard. Finally, a related issue concerns sample selection bias. We utilized all of the large undergraduate data sets we possess that included the DSQ, PVD, HBI or BIS, alongside data we could find from published reports that included subscale means, standard deviations and gender distributions, drawn from demographically, culturally and linguistically similar cohorts (i.e., undergraduates from English speaking countries).

Our contention is that the consistent effects observed for core disgust, and to some extent germ aversion, reflect reactions to the Covid-19 pandemic rather than some other unrelated cohort difference. On an individual level the pandemic involves exposure to unremitting media coverage of the pandemic (both reassuring, fear provoking and factual in content), physical and social isolation, potential loss of income, large alterations inbehavior (e.g., distancing, hand hygiene, home learning) and heightened vigilance to disease-relevant cues. We suggest that the import of these changes results in up-regulated disgust sensitivity and to some extent germ aversion. Both of these constructs are strongly related (Cohen's d = 1.2) and both were also found to be increasing across the course of the survey period. This latter effect can be regarded as akin to a dose-response effect, with those completing the survey toward the end of the study period exposed to cumulatively more of the Covid-19 pandemic than those completing it early on.

One consideration is the functional import of increases in disgust sensitivity and relatedly, germ aversion. First, it is apparent from **Table 2** that both disgust sensitivity and germ aversion are higher in individuals who report greater levels of hygiene behavior. Experimental tests suggest that disgust-based interventions both in the laboratory and real-world settings can produce increases in hand-hygiene behavior (Porzig-Drummond et al., 2009; Pellegrino et al., 2016). In addition, women in both laboratory and naturalistic settings wash their hands more frequently than men (e.g., Porzig-Drummond et al., 2009; Filion et al., 2011; Prokop et al., 2014). As we noted in this report and as widely documented elsewhere, women also report being more disgust sensitive than men (Al-Shawaf et al., 2018) and in addition, in the current study, women also reported higher rates of illness in the preceding week than men (15 vs. 4%). The combined consequence of these effects may be to increase the tendency to engage in hand-hygiene. A second consequence may relate to food. While reported increases in general hygiene and hand hygiene technique in the MU20 sample were predictable, as these measures primarily relate to hand washing, we also observed a robust increase in food-related hygiene too (Cohen's d = 0.4) - yet this subscale has only one hand washing item. Disgust has often been conceptualized has having its phylogenetic roots in food avoidance (Rozin et al., 2016) and so a further consequence of increasing disgust sensitivity may be greater wariness around eating and food preparation. Third, as we noted at the start of the manuscript, disease inductions affect a wide variety of behaviors that are purported to improve disease avoidance (Faulkner et al., 2004; Lee et al., 2010; Prokop and Fancovicova, 2010; Murray and Schaller, 2012; Murray et al., 2013). While there has been some interest in identifying if the PVD serves to moderate these effects – and there is some evidence

that it does (Murray et al., 2013) – it is not currently known if this also holds for disgust. If it does, then enhanced disgust sensitivity might also facilitate, these broader types of avoidant behavior.

A further question is *how* the various experiences that comprise the Covid-19 pandemic drive up disgust sensitivity and in particular *what* specific aspects of the experience might be responsible? As the average increase in disgust sensitivity would be quite small, it would presumably not be self-evident (in contrast to knowing that a pandemic was underway etc.), suggesting it might be an implicit change (or consistent with Pinker (1997), p383] - disgust as an intuitive microbiology). Finally, we also tentatively suggest that just as pain is more intense when it is perceived as threatening (e.g., a pain *may* mean irreparable tissue damage or just a bruise; Jackson et al., 2014), the same may also hold for disgust (Stevenson et al., 2019). It would seem reasonable to presume that the level of threat that people perceive during the Covid-19 pandemic would be far higher than normal and so this could in turn increase the intensity of disgust sensitivity. The arguably parallel finding in the pain literature is highly robust (Jackson et al., 2014).

In conclusion, we find that relative to earlier undergraduate cohorts - and assuming their similarity in most other regards – the MU20 sample who completed disgust sensitivity and other measures during the lockdown period of the Covid-19 pandemic, report higher disgust sensitivity, possibly greater germ aversion, an increase in safety behavior (hand washing), but with little change in impulsivity. We suggest that the putative increases in disgust sensitivity may have several functional benefits, and that the increase in disgust sensitivity arises implicitly from the threat of the Covid-19 pandemic.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusion of this article will be made available by the authors on request.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Macquarie University Human Research Ethics Committee. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

RS and TC conceived the study. RS analyzed the data and drafted the manuscript. SS undertook the data collection. TC and SS reviewed and revised the manuscript. All authors contributed to the article and approved the submitted version.

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REVIEW
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Pandemic Leadership: Sex Differences and Their Evolutionary–Developmental Origins

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The COVID-19 pandemic has caused a global societal, economic, and social upheaval unseen in living memory. There have been substantial cross-national differences in the kinds of policies implemented by political decision-makers to prevent the spread of the virus, to test the population, and to manage infected patients. Among other factors, these policies vary with politicians' sex: early findings indicate that, on average, female leaders seem more focused on minimizing direct human suffering caused by the SARS-CoV-2 virus, while male leaders implement riskier short-term decisions, possibly aiming to minimize economic disruptions. These sex differences are consistent with broader findings in psychology, reflecting women's stronger empathy, higher pathogen disgust, health concern, care-taking orientation, and dislike for the suffering of other people—as well as men's higher risk-taking, Machiavellianism, psychopathy, narcissism, and focus on financial indicators of success and status. This review article contextualizes sex differences in pandemic leadership in an evolutionary framework. Evolution by natural selection is the only known process in nature that organizes organisms into higher degrees of functional order, or counteracts the unavoidable disorder that would otherwise ensue, and is therefore essential for explaining the origins of human sex differences. Differential sexual selection and parental investment between males and females, together with the sexual differentiation of the mammalian brain, drive sex differences in cognition and behavioral dispositions, underlying men's and women's leadership styles and decision-making during a global pandemic. According to the *sexually dimorphic leadership specialization hypothesis*, general psychobehavioral sex differences have been exapted during human evolution to create sexually dimorphic leadership styles. They may be facultatively co-opted by societies and/or followers when facing different kinds of ecological and/or sociopolitical threats, such as disease outbreaks or intergroup aggression. Early evidence indicates that against the invisible viral foe that can bring nations to their knees, the strategic circumspection of empathic feminine health "worriers" may bring more effective and humanitarian outcomes than the devil-may-care incaution of masculine risk-taking "warriors".

Keywords: COVID-19, sex differences, cognition, leadership, pandemic, population health, evolution, sexually dimorphic leadership specialization

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INTRODUCTION

The novel coronavirus and the disease that it causes (i.e., COVID-19) created a social and economic upheaval unseen in the past half a century or more. The political and social responses to the COVID-19 pandemic, as well as the SARS-CoV-2 virus itself, have both had major effects on economic activity, public policy, civic engagement, and population health almost all over the world (Bedford et al., 2020; Weible et al., 2020). Being under direct human control, such policy responses (versus inaction) have the potential to diminish the impact of the virus or to amplify its disastrous effects.

We review the evidence on cross-national differences between male and female leadership during the pandemic and discuss the possible evolutionary–developmental and psychobehavioral mechanisms underlying such differences (**Figure 1**). Based on a review of relevant research in evolutionary science, psychology, behavioral science, anthropology, political science, economics, behavioral genetics, and developmental, cognitive, and behavioral neuroscience, we also present the *sexually dimorphic leadership specialization hypothesis* as one of the possible explanations for these cross-national patterns.

PUBLIC POLICY RESPONSES TO THE COVID-19 PANDEMIC

An increased consensus has emerged on how to effectively manage the COVID-19 pandemic and the transmission of the SARS-CoV-2 virus (Habersaat et al., 2020; Kaplan et al., 2020; Priesemann et al., 2021). Countries have implemented a range of measures to curb the spread of the virus (Bedford et al., 2020); while some countries have implemented strict measures that have shut public life and most commercial activity almost completely, others have kept significant parts of society open even though faced with similar health threats imposed by SARS-CoV-2. Research into the factors that predict cross-national differences in pandemic responses and subsequent outcomes has been conducted during the pandemic's global spread (Coelho et al., 2020; Puterman et al., 2020; Salvador et al., 2020), and among other factors (cf. Burkle, 2020; Windsor et al., 2020; Krams et al., 2021), political leaders' sex hypothetically contributes to cross-national variation in pandemic outcomes.

SEX DIFFERENCES IN PANDEMIC LEADERSHIP AND CROSS-NATIONAL COVID-19 OUTCOMES

To provide a prominent example, Brazil's President Jair Bolsonaro has mostly downplayed the COVID-19 health threat and has implemented less severe societal measures than many other political leaders in the first months of the pandemic (Ponce, 2020). When asked about the rapidly rising cases of COVID-19 victims in Brazil in May 2020, President Bolsonaro responded with a callous "So what? What do you want me to do?", whilst continuing to flout and discourage physical distancing and lockdown policies (Prado, 2020). When infected with SARS-CoV-2, he broke quarantine regulations to ride a motorcycle and interacted mask-less with people. With 746 COVID-related deaths per million inhabitants by October 30th 2020, Brazil was ranked the country with the 6th most COVID-related deaths (for details, see **Supplementary Materials**).

Other political leaders have taken the opposite approach. New Zealand implemented draconian lockdown measures at a stage when there were only 102 confirmed COVID-19 cases and no reported deaths on March 23rd 2020. The Prime Minister, Jacinda Ardern, emphasized the importance of early, preventative action in her address to the citizens of New Zealand on the eve of societal lockdown: "act now, or risk the virus taking hold, as it has elsewhere [. . .] the situation here is moving at pace, and so must we [. . .] together, we must stop [the virus from spreading and killing tens of thousands of New Zealanders]. Now is the time to act" (Ardern, 2020). Her approach was so successful that her popularity skyrocketed, leading to a landslide victory for her party in the New Zealand parliamentary election in October 2020. With five COVID-related deaths per million inhabitants by October 30th 2020, New Zealand had one of the lowest mortality rates globally (**Supplementary Materials**).

Garikipati and Kambhampati (2020) examined the association between political leaders' sex and variation in pandemic responses and outcomes across 194 countries (19 of which were coded as female-led). Female leaders, on average, reacted more quickly and decisively to the COVID-19 pandemic than their male counterparts, implementing measures that resulted in lower mortality rates (Garikipati and Kambhampati, 2020). These results remained robust when controlling for country-level annual health expenditure, openness to tourists, Gender Inequality Index (a measure of women's versus men's participation in politics and the labor force), per capita gross domestic product (GDP), population size, urbanization, and population over 65 years of age. This preliminary analysis was based on total deaths and total cases due to COVID up to May 19th 2020, and therefore covered only the first months of the pandemic. However, a cross-national study including 15 female-led countries found no country-level differences based on leaders' sex in time to implementation for any of the most common COVID-19 containment policies: stay-at-home orders, school closings, public information campaigns (Aldrich and Lotito, 2020), indicating that female leaders were (statistically) no quicker than male leaders to implement such measures. Nevertheless, 63% of women-led countries, as opposed to only about half of all countries, launched coordinated information campaigns before their first confirmed case of COVID-19, and average time to implementation was one week shorter in women-led countries than in male-led ones (Aldrich and Lotito, 2020).

Another study of 159 countries found that female-led countries had lower median case-fatality rates relative to male-led countries through June 3rd 2020; however, because of the small sample of female-led countries (n = 18), the difference did not reach conventional levels of statistical significance (Purkayastha et al., 2020). The results are nevertheless

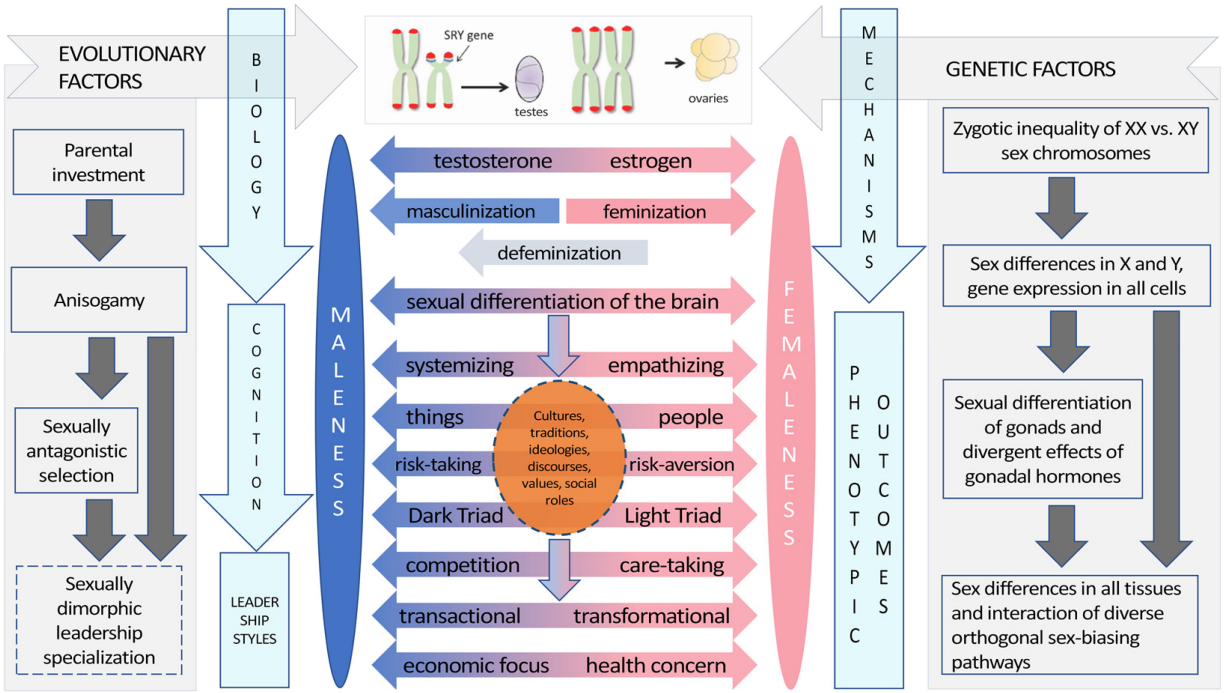

FIGURE 1 | The evolutionary–developmental origins and proximate mechanisms underlying psychobehavioral sex differences, including those in leadership. Sexually dimorphic leadership specialization is included as a new hypothesis, not as an established fact. Figure adapted from Luoto et al. (2019a), Arnold (2020), McCarthy (2020), and Malmi (2021).

suggestive[1]. These patterns in male-led and female-led countries are visualized in **Figure 2**, which shows global COVID-19 deaths per 1 million inhabitants as a factor of the Human Development Index (HDI), using more recent data than Purkayastha et al. (2020) and Garikipati and Kambhampati (2020)[2]. The data points are colored to reflect the sex of each country's leader, and scaled according to COVID-19 testing rates per 1 million inhabitants. For higher granularity, **Figure 3** shows the same outcomes only in Europe[3].

The relationship between leader's sex and a population's COVID-19 outcomes has also been studied at the level of states in the United States. As of May 5th 2020, states (N = 55, comprising 50 states, the District of Columbia, and four American Territories) with female governors had fewer COVID-19 deaths than states with male governors (Sergent and Stajkovic, 2020). States with women governors who issued early stay-at-home orders also had fewer deaths compared to states with men governors who issued similar orders (Sergent and Stajkovic, 2020). The study controlled for governor's political affiliation (Sergent and Stajkovic, 2020), but not for other biodemographic variables such as state-level rates of obesity, smoking, or age structure, which could all have influenced differences in COVID-19 outcomes between states (Jordan et al., 2020; Krams et al., 2020). The results are nevertheless in line with the cross-national data. Furthermore, a psycholinguistic analysis of 251 briefings from 38 different state governors comprising 1.2 million words indicated that female governors, relative to male governors, showed more empathy via greater awareness of the feelings of others (Sergent and Stajkovic, 2020). Female governors also spoke more about work and money, perhaps to reassure followers that there is a brighter future ahead. South Dakota Governor Kristi Noem, for instance, noted in her address on April 6th 2020 that "resources are available to you, whether it be economic or mental health and labor unemployment" (Sergent and Stajkovic, 2020)[4].

Generally, some of the leaders who have shown the strictest, most humanitarian responses to the pandemic are females (e.g., Jacinda Ardern in New Zealand, Katrín Jakobsdóttir in Iceland, Sanna Marin in Finland), while the most indifferent

[1]We note the publication of a third cross-national study by Windsor et al. (2020), which did not find significant differences in the proportion of deaths for the group of countries with female leaders relative to the group of countries with male leaders. This null finding could have been partially driven by the low statistical power, as Windsor et al. (2020) included only 12 female-led countries (and 155 male-led countries) in their analyses.

[2]Data on total COVID-19 deaths and COVID-19 tests per 1 million inhabitants up to October 30th 2020 were collected from the Worldometer site (https://www.worldometers.info/coronavirus/#countries). Human Development Index data were collected from United Nations Development Programme (http://hdr.undp.org/en/content/human-development-index-hdi). The Human Development Index is a composite index of life expectancy at birth, education, and per capita income.

[3]That Belgium is such a stark outlier amongst women-led countries could be because Belgium's high numbers may have been driven by including also suspected (rather than only confirmed) cases in the total count of COVID-19 deaths (Windsor et al., 2020).

[4]Though otherwise Noem's approach may have been somewhat lax owing to her refusal to mandate mask use.

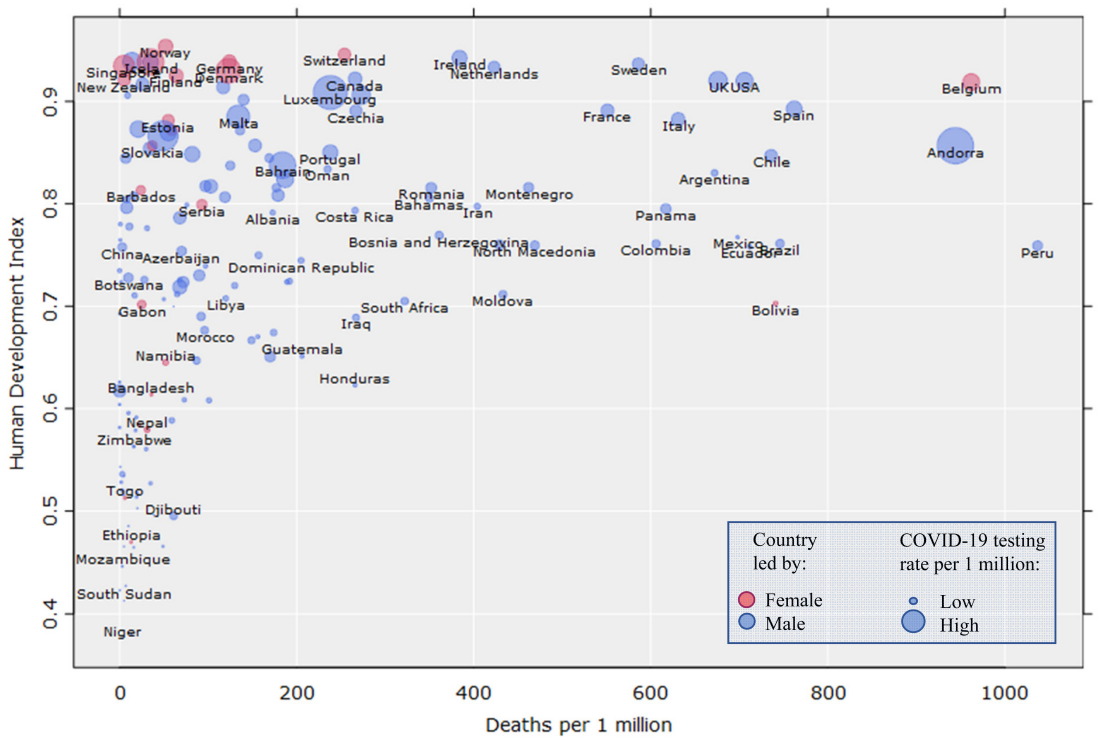

FIGURE 2 | COVID-19 deaths per 1 million in relation to the Human Development Index (N = 168, r_s = 0.51). Data points are colored according to the sex/gender of the country leader, and scaled to COVID-19 tests per 1 million. For the full data, see **Supplementary Materials**.

or even reckless responses have been made by male leaders (e.g., Jair Bolsonaro in Brazil and Stefan Löfven and the state epidemiologist Nils Anders Tegnell in Sweden) (**Figures 2**, **3**). The 2020 Ig Nobel prize in "Medical Education" was awarded to a group of male political leaders "for using the Covid-19 viral pandemic to teach the world that politicians can have a more immediate effect on life and death than scientists and doctors can" (Tanne, 2020)[5]. The world leaders edition of the *BMJ* "COVID-19 yearbook" also confirms this same pattern (Looi, 2020). Overall, leadership style, communication, and policy-making during pandemics are important for population-level outcomes because trust in authorities has a positive effect on the adoption of many protective behaviors (Gong et al., 2020; see also Haslam et al., 2021).

PSYCHOBEHAVIORAL SEX DIFFERENCES

Psychological sex differences, such as men's higher risk-taking, systemizing, and things orientation—and women's higher fearfulness, empathizing, and people orientation—have been reported in a variety of domains (Geary, 2010; Christov-Moore et al., 2014; Varella et al., 2016; Greenberg et al., 2018; Archer, 2019; Luoto, 2020), and may be instrumental in decision-making in a high-pressure leadership context (Sweet-Cushman, 2016). The multivariate space of personality differences between men and women has been measured as D = 2.71 (in a US sample), corresponding to an overlap of only 10% between male and female personality profiles, assuming statistical normality (Del Giudice et al., 2012). In some cases, male and female political leaders' responses to the COVID-19 pandemic may reflect a similar kind of difference. We should also note, however, that such generalizations represent average sex differences and that individual variation within each sex tends to be larger than differences between the sexes (Archer, 2019; Del Giudice, 2019; Luoto et al., 2019a). It is also possible that executive positions have a homogenizing effect on personality whereby psychologically more male-typical women pursue and are chosen for leadership positions (Wille et al., 2018). We return to these issues at the end of this article after reviewing research on psychobehavioral sex differences in this section, and their evolutionary–developmental origins in the next section.

Personality

Systemizing–empathizing is a sexually dimorphic cognitive dimension which is highly relevant to leadership and decision-making. *Systemizing* refers to the tendency to build a rule-based system, to see patterns in systems, and/or to understand how

[5]The male leaders were: Jair Bolsonaro of Brazil, Boris Johnson of the United Kingdom, Narendra Modi of India, Andrés Manuel López Obrador of Mexico, Alexander Lukashenko of Belarus, Donald Trump of the United States, Recep Tayyip Erdogan of Turkey, Vladimir Putin of Russia, and Gurbanguly Berdimuhamedow of Turkmenistan.

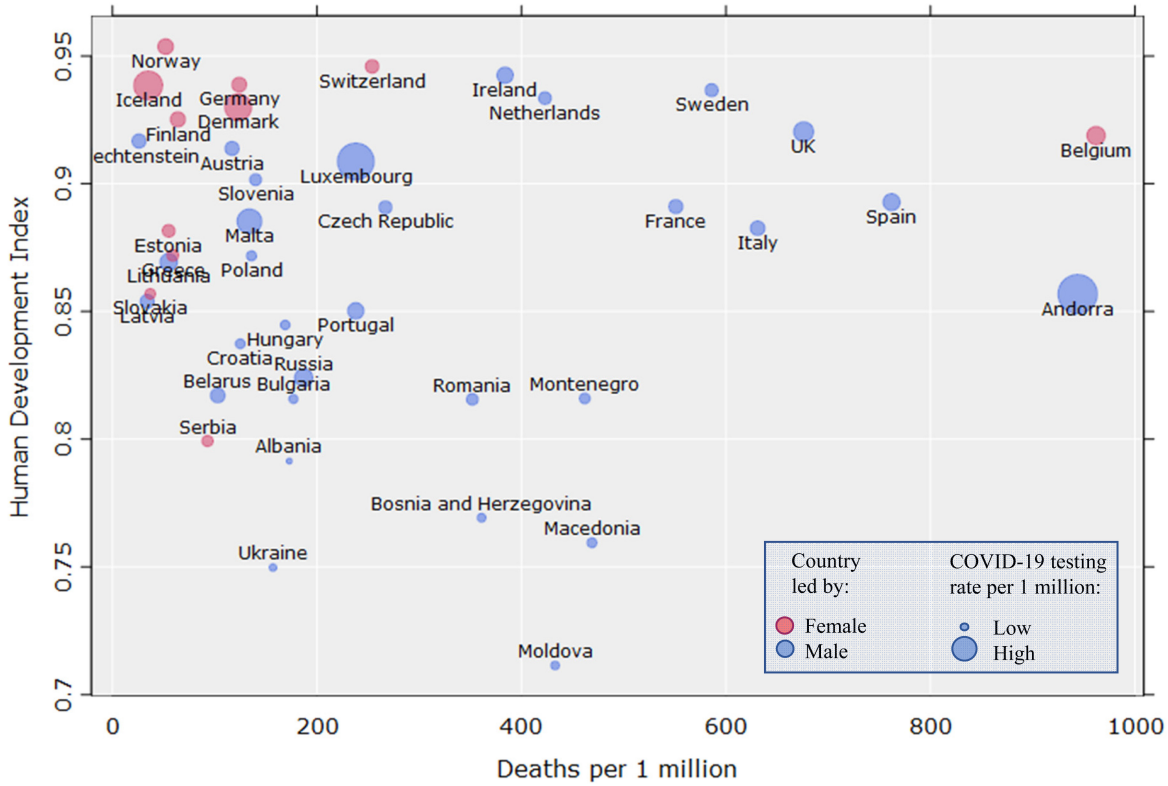

FIGURE 3 | COVID-19 deaths per 1 million in relation to the Human Development Index in European countries (n = 41, r_S = –0.07). Data points are colored according to the sex/gender of the country leader, and scaled to COVID-19 tests per 1 million.

such rule-based systems work. *Empathizing* refers to the ability to recognize another person's mental state ("cognitive empathy") and the tendency to respond to it with an appropriate emotion (Greenberg et al., 2018; Archer, 2019). Men tend to score higher on systemizing (Cohen's *d*s are generally medium to very large, ranging between 0.31 and 1.21), while women, on average, have higher scores on empathizing (Cohen's *d*s generally ranging between –0.39 and –0.87) (Greenberg et al., 2018; Archer, 2019; see also Löffler and Greitemeyer, 2021).

Sex differences in people and things orientation are found across various psychobehavioral domains. Findings consistently show that women, on average, perceive and orient toward people with greater psychological interest, whereas men, on average, are psychobehaviorally more oriented toward objects than women are (Su et al., 2009; Archer, 2019; Luoto, 2020). The degree to which men and women differ in the psychological salience of people vs. objects (d = –0.93 in a meta-analysis), and how it affects men's and women's behavior and decision-making (Archer, 2019; Luoto, 2020), is relevant in a pandemic leadership context. These psychological sex differences may make cautious, humanitarian responses more natural to female leaders, while male leaders may be more concerned with retaining the integrity of the socioeconomic system.

There are several other personality differences between men and women which may make female leaders' responses to the pandemic more humanitarian. On average, men have lower fear in real-world situations (d = –1.16), lower social interests (d = –0.68), social leadership (d = –0.18), peer attachment (d = –0.51), guilt (d = –0.27), and emotional intelligence (d = –0.47) than women (Archer, 2019). Across cultures, women have higher average levels of neuroticism (the tendency to experience negative emotions) than men, with overall effect sizes averaging d = –0.40 (Schmitt et al., 2008; Kajonius and Johnson, 2018; Archer, 2019). Women also tend to exhibit higher anxiety (d = –0.59), agreeableness (d = –0.29), and conscientiousness (*d*s from –0.12 to –0.21)[6] than men (Schmitt et al., 2008; Archer, 2019; Allen and Robson, 2020).

More neurotic individuals tend to be hypervigilant, experience anticipatory anxiety, and threat sensitivity (Barlow et al., 2014). More agreeable individuals tend to exhibit higher altruism, tender-mindedness, and health consciousness. Individuals with high conscientiousness exhibit self-discipline, are aware of their responsibilities toward society, and show more health consciousness (Kaynak and Ekşi, 2014). Neuroticism, agreeableness, and conscientiousness are among the personality traits related to compliance with the shelter-in-place measures during the COVID-19 pandemics (Götz et al., 2020). Neuroticism is also related to more concerns but fewer COVID-19

[6]These effect sizes are respectively from Schmitt et al. (2008) and Allen and Robson (2020, based on the reported raw means and standard deviations). Notably, others have argued that sex differences in conscientiousness are confined to just some of its components (Del Giudice et al., 2012).

precautions, while conscientiousness is associated with more precautions during pandemics (Aschwanden et al., 2020).

Leadership

Research on leadership styles suggests that women are more communal, intuitive, sensitive, and empathetic as leaders than men (Rosette and Tost, 2010; Peterson and Bartels, 2017). A meta-analysis found that women tend to exhibit a transformational leadership style which is more relationship-oriented, whereas men tend to show a transactional leadership style which is more task-oriented (Eagly et al., 2003). Men's leadership is characterized by waiting for problems before innovating solutions, which is consistent with waiting until disaster exacerbates before implementing relief measures (Windsor et al., 2020). Men, on average, tend to prefer having power (defined as control over valued resources) and being feared, while women tend to prefer status (defined as the extent to which one is respected by others) and being loved (Hays, 2013). Female leaders were reportedly rated as less feared than female non-leaders in a forager-horticulturalist population (Garfield and Hagen, 2020). Female leaders are also more likely to navigate social situations successfully and to adapt their behavior accordingly, whilst male leaders, on average, may have a higher likelihood of inflexibly "staying the course" regardless of contextual cues (Peterson and Bartels, 2017). In a pandemic situation, such inflexibility may be catastrophic, as contextual cues from scientists, as well as learning about the outcomes of the pandemic in other countries, can clearly show that inaction—failing to impose measures to stop the virus from spreading—can have worse consequences than imposing societal policies designed to curb the spread of the virus (Haug et al., 2020). On the other hand, the full economic consequences of lockdown policies are also yet to be determined, and may in some cases offset some of the immediate benefits that such policies accrue to population health.

Competitiveness

Sex differences in competitiveness have been consistently documented in children and adults. Men tend to be more competitive than women across a range of tasks both in large-scale post-industrial societies and in hunter-gatherers (Grainger and Dunbar, 2009; Frick, 2011; Apicella and Dreber, 2015; Hone and McCullough, 2015; Martin, 2020). Studies on competitiveness involving negotiation and bargaining—conducted using laboratory measures of dyadic interactions between North American students—have reported no sex differences in competitiveness, possibly because such contexts are very different from the concept of competition in an evolutionary sense, and from real-life competitiveness for status/power and for attracting a sexual partner (Archer, 2019). Real-life conversations between two males, however, involved much more competitive communication, both verbal and non-verbal, than those between two females, as reported in a study in the United Kingdom (Grainger and Dunbar, 2009). Women are, on average, less willing than men to enter competitive situations, partially because women may be less capable than men in some competitive environments, especially when competing against the opposite sex (Hessami and da Fonseca, 2020; see also Archer, 2019). Even when men and women have similar abilities, men still prefer competition at a much higher rate than women (Hessami and da Fonseca, 2020). A study on the Hadza hunter-gatherers in Tanzania reported that men's higher competitiveness manifests particularly in male-centric and neutral tasks, whereas in female-centric tasks there is no sex difference in competitiveness (Apicella and Dreber, 2015). Another study conducted in Spain reported that when there was status ranking in a competitive cognitive task, men significantly increased their competitiveness and performance and women significantly decreased their competitiveness; in the absence of status ranking, however, there were no sex differences in competitiveness or performance (Schram et al., 2019). In contrast, when competition is not for money but directly benefits the participants' children, sex differences in competitiveness disappear, as observed in a study in China (Cassar et al., 2016). A study on children and adolescents from a lower socio-economic segment of Turkey reported that in childhood, there was no significant sex difference in willingness to be a group leader; however, in adolescence, girls became less willing than boys to take on leadership roles, partially because girls had lower self-confidence and social confidence (Alan et al., 2020). One psychological mechanism associated with these sex differences is that girls experience greater competition-induced discomfort than boys in competitive situations, even when competing with same-sex peers (Benenson et al., 2002).

Risk-Taking

Female leaders' initial success in tackling the pandemic may be caused in part by women's greater risk aversion and men's greater risk-taking (Archer, 2019; Garikipati and Kambhampati, 2020). Men, on average, tend to score higher than women in risk-taking tasks (d = 0.49), while women, on average, score higher than men in harm avoidance (d = –0.33) (Archer, 2019; see also Ertac and Gurdal, 2012; Gong and Yang, 2012). A study on Israeli executives' leadership orientations reported that women demonstrated better crisis preparedness by adopting a more holistic approach toward handling crises (Mano-Negrin and Sheaffer, 2004). Similar findings have been reported from hunter-gatherers to bank CEOs. Tanzanian hunter-gatherer males take more risks than females, even as early as in late childhood (Apicella et al., 2017). An analysis of the leadership of S&P 500 firms (n = 391) found that firms with female chief financial officers were associated with income-decreasing discretionary accruals, which is in line with sex differences in financial conservatism, risk-aversion, and managerial opportunism (Peni and Vähämaa, 2010). Similarly, a study on 6,971 American commercial banks reported that banks with female CEOs and board chairs were associated with better lending performance and lower default risk in the aftermath of severe real estate price shocks relative to male-led banks, suggesting that female leadership may lead to less risky corporate outcomes (Palvia et al., 2020). These findings are corroborated by a study on Norwegian firms, which reported that introducing gender-balancing quotas that increased women's representation as firm directors significantly reduced firm risk, though it adversely affected the performance of firms (Yang et al., 2019). A study on

company team leaders from the US reported lower risk-taking in female team-leaders relative to males, while innovation scores were lower in female-led teams regardless of the team members' sex (Zuraik et al., 2020). A meta-analysis has shown that sex differences exist in virtually every area in which risk has been studied, with males engaging in more risk-taking than females (Byrnes et al., 1999). A Swiss study reported that male risk-taking was higher than baseline risk-taking in men in the presence of a male social partner (d = 0.87) but not in the presence of a child or a female. Women's risk-taking was uninfluenced by the presence of other adult males or females; however, in the presence of a baby, women's risk-taking was substantially lower (d = –0.71) from their non-social baseline (Fischer and Hills, 2012). These findings suggest a degree of sex-specific context-sensitivity in men's and women's risk-taking, with men's risk-taking increased by the presence of another man and women's risk-taking decreased by the presence of a child.

Nevertheless, even when female leaders minimize risks of human suffering by imposing stricter policy measures, such as nation-wide lockdowns, such decisions inevitably lead to greater *short-term* economic risk-taking relative to male leaders (Garikipati and Kambhampati, 2020). Since women's risk aversion is related to reducing risk of physical harm to themselves and their family and friends (Geary, 2010), and since men are more focused than women on status-seeking (Geary, 2010; Sweet-Cushman, 2016; Archer, 2019; Benenson and Abadzi, 2020), men may be more likely to prioritize immediate economic goals over attempts to minimize health-related risks to others[7]. Furthermore, because women, on average, are more people-oriented, while men, on average, tend to be more things-oriented—and because women have higher empathizing cognitive styles than men (Greenberg et al., 2018; Archer, 2019; Luoto, 2020)—the risks that female leaders view with human suffering may be more salient for them than the risks that female leaders associate with the economy[8]. Economy is more removed from direct human experience and, as an abstract high-level rule-based system, may thus be cognitively more prominent to male leaders, on average, because of men's higher systemizing cognitive styles (Chari and Goldsmith-Pinkham, 2017; Greenberg et al., 2018; Archer, 2019; Bosquet et al., 2019; Luoto, 2020). Increasing the representation of women in policymaking bodies does not appear to change overall public expenditure; however, higher representation of women in local councils accelerates the expansion of public child care provision and leads to more frequent council discussions on child care (Hessami and da Fonseca, 2020). Furthermore, as men tend to orient toward economic conservatism and women tend to be economically more progressive (i.e., to support policies aimed at equalizing wealth) (Pratto et al., 1997; Harteveld et al., 2019; Hessami and da Fonseca, 2020), it is possible that male political leaders are more concerned about maintaining the economic *status quo* than female leaders. This tendency could result in male leaders being less likely than females to impose lockdowns which restrict economic activity.

Behavioral Responses to Psychosocial Stress

This view is further supported by sex differences in behavioral responses to psychosocial stress. When experiencing acute psycho-physiological stress, women are more likely to show cooperative behavior which is consistent with the 'tend and befriend' hypothesis, while men are more likely to become selfish and competitive, thus showing signs of the 'fight or flight' response (Nickels et al., 2017; see also Youssef et al., 2018). More specifically, when exposed to psychosocial stress, males' tendency to cooperate either did not change or decreased (Nickels et al., 2017; Youssef et al., 2018). Stressed males made lower monetary offers than control men to their partners and tended to behave less prosocially in a risky and potentially dangerous situation, which involved a person in need of help (Nickels et al., 2017). Stressed women, in contrast, offered higher monetary amounts in an economic game and behaved more cooperatively in Prisoner's Dilemma game compared with control women (Nickels et al., 2017). As with sex differences in pandemic leadership, these results showed a 'tend and befriend' response in stressed females as they became more other-oriented, more generous, and more cooperative, while the behavior of males exposed to stress showed signs of the 'fight or flight' response.

Dark Triad and Light Triad

Antisocial personality traits known as the Dark Triad traits (Machiavellianism, narcissism, and psychopathy) may also be highly relevant in a pandemic context, which calls for coordinated, cooperative, and unselfish action. Machiavellianism is associated with manipulative and exploitative behaviors, self-interest, and a ruthless lack of morality; narcissism is characterized by a sense of grandiosity, egotism, and self-orientation; and psychopathy entails antisocial behavior, impulsivity, and a lack of empathy and remorse (Koehn et al., 2018). Men have slightly higher scores on the Dark Triad personality traits than women: cross-national research has revealed small (Cohen's $d \approx 0.20$) to large ($d \approx 0.70$) sex differences in the Dark Triad traits, though the effects are primarily driven by men's higher psychopathy relative to women (Jonason et al., 2013, 2017; Muris et al., 2017). The Dark Triad traits are positively correlated with dominant leadership, ruthless self-advancement, and prejudice, and negatively correlated with coalition-building (Semenyna and Honey, 2015; Koehn et al., 2018). Psychopathy is also negatively associated with parental investment (Valentova et al., 2020). In the context of the COVID-19 pandemic, individuals with higher Dark Triad traits were less

[7]Many of the papers on the evolution of leadership (e.g., von Rueden et al., 2018; Garfield et al., 2019b) or on the evolution of sex differences (e.g., Archer, 2019) do not provide an explicit definition of 'status'. Some papers do define 'status', but the definitions are not always similar. For example, in Hays (2013), 'status' was defined as the extent to which one is respected by others. In von Rueden et al. (2011), 'social status' was defined as relative access to contested resources within a social group. Garfield et al. (2019a) defined status/prestige as an individual's value based on subjective evaluations by the group. For this reason, we have not relied on a single definition of 'status', but have chosen instead to highlight variation and/or ambiguity in its usage in relevant literature.

[8]In the long run, it is possible that the best population-health response is also the best economic response, as a society that has eliminated the virus may be better able to resume healthy economic activity. This remains to be empirically confirmed.

likely to comply with the pandemic restrictions (Zajenkowski et al., 2020) and exhibited less prevention and more hoarding (Nowak et al., 2020).

Kaufman et al. (2019) sought to conceptualize whether there is a complementary set of attributes besides the Dark Triad traits that predicts prosocial rather than antisocial outcomes. The factor-analytically derived Light Traits measure loving and beneficent orientation toward others. The Light Triad consists of three facets: Kantianism (treating people as ends unto themselves), Humanism (valuing the dignity and worth of each individual), and Faith in Humanity (believing in the fundamental goodness of humans). Females had lower scores on the Dark Triad traits (r = –0.28) than males, while the Light Triad traits were more common in females than in males (r = 0.20). These correlations remained robust even after controlling for agreeableness (Kaufman et al., 2019), but they await replication in other samples as the Light Triad is a more recent addition to the sex difference literature than Dark Triad. Overall, sex differences in Light Triad and Dark Triad traits may influence the extent to which male leaders fail to minimize direct human suffering caused by the pandemic.

Pathogen Disgust, Health Concern, and Health Behaviors

Importantly for decision-making in a pandemic context, women have higher pathogen disgust than men both generally (Al-Shawaf et al., 2018) as well as in the COVID-19 context (Stevenson et al., 2021), suggesting that women's decision-making may seek to minimize the spread of a deadly virus more than men's. The emotion of disgust has far-reaching implications for several areas of psychology, from cognition, judgment, decision-making, and social relationships to health and other behaviors (Al-Shawaf et al., 2018), and so it may be reflected in the decisions that women make even at relatively high levels of abstraction when faced with a pathogenic threat. During the COVID-19 pandemic, women in the general public showed more concern about their own and others' health (Prichard and Christman, 2020), wearing masks 1.5× more frequently than men (Haischer et al., 2020), even though COVID-19 disease severity and mortality are higher in men (Krams et al., 2020). These sex differences extend even to dreams during the COVID-19 pandemic: a cross-national study on 1,998 women and 890 men reported that women showed significantly lower positive emotions in their dreams and higher rates of negative emotions, anxiety, sadness, anger, body content, and references to biological processes, health, and death than men (Barrett, 2020).

Women also expressed more concern about the financial wellbeing of others than men did (Prichard and Christman, 2020). Survey data from eight countries indicated that women were more likely than men to perceive COVID-19 as a very serious health problem, to agree with restraining public policy measures, and to comply with them (Galasso et al., 2020). A study including 101,005 participants from 55 countries showed that men were more likely to take the risk of going outdoors and were less likely to shelter-in-place than women during the early stages of the pandemics (Götz et al., 2020). A study conducted mainly on Russian participants during the COVID-19 pandemic reported that women had a higher level of anxiety and lower level of spatial mobility than men, suggesting that women take fewer risks by minimizing their mobility during the pandemic (Semenova et al., 2021). A meta-analysis of 85 studies on sex differences in protective behaviors in response to respiratory epidemics and pandemics pre-COVID-19 showed that women were 50% more likely than men to adopt/practice non-pharmaceutical behaviors, such as hand washing, face mask use, and avoidance of public transport (Moran and Del Valle, 2016). A study unrelated to the pandemic context reported that across 67 countries, women showed higher dislike for the suffering of others, as well as more concern about physical and spiritual purity and contamination than men (Atari et al., 2020). Moreover, women with obsessive-compulsive disorder present more contamination/cleaning symptoms while male patients present more sexual-religious and aggressive symptoms (Mathis et al., 2011). In the aggregate, these findings provide additional evidence for the way in which women's higher empathy, pathogen disgust, care orientation, health orientation, risk aversion, and neuroticism manifest in a pandemic context.

EVOLUTIONARY–DEVELOPMENTAL ORIGINS OF SEX DIFFERENCES

Complete evolutionary biological explanations of behaviors or traits need to address four levels of analysis—phylogeny, ontogeny, proximate mechanisms, and ultimate function(s). These can be formulated into four questions concerning any feature of an organism. Answers to these "Tinbergen's four questions" can be synthesized into a common explanatory framework elucidating the evolutionary origins and biological mechanisms underlying behaviors or traits (Tinbergen, 1963; Luoto et al., 2019a). In this section, we briefly provide such a four-level analysis on sex differences in humans.

Ultimate Functions

Evolution by natural selection is the only known natural process that propels organisms into higher degrees of functional order, or counteracts the unavoidable increase in disorder that would otherwise ensue (Tooby et al., 2003; Tooby, 2020). All functional organization in undomesticated organisms that is greater than could be expected by chance ultimately results from natural selection and therefore needs to be explained with recourse to it (Tooby et al., 2003; Lewis et al., 2017; Buss, 2020; Tooby, 2020). As living beings, humans are also subjected, body and mind, to the same evolutionary processes as other species. Evolution by natural selection therefore enables a deeper understanding of the origins of human behavior, including sex differences (Archer, 2019; Luoto, 2019; Buss, 2020; Tooby, 2020) and leadership (Sweet-Cushman, 2016; Garfield et al., 2019b; Smith et al., 2020; Van Vugt and von Rueden, 2020). Many factors on different levels, from genetics, local ecology, individual development to social history and phylogenesis, may concomitantly influence the degree of sexual differentiation. Although evolutionary theory provides only a part of the explanation for sex differences,

that part is fundamental, offers heuristic power, and helps to reorganize factors that otherwise appear disconnected (DeBruine, 2009; Lewis et al., 2017; Archer, 2019; Luoto, 2019; Buss, 2020).

For instance, natural selection is not separate from cultural explanations of behavior (**Figure 1**), as "cultural" practices, such as sexual division of labor, are not purely cultural but arise partially because of evolutionary selection pressures acting on sexually dimorphic physiology, cognition, and behavior (Janicke et al., 2016; von Rueden et al., 2018; Archer, 2019). A broader empirically grounded and mechanistic picture on the evolution of sex differences can be acquired from cross-species research on the neurodevelopmental mechanisms that drive sexual differentiation of the brain and behavior (Luoto et al., 2019a; Arnold, 2020; Liu et al., 2020; McCarthy, 2020), a matter to which we return in the section titled "Proximate mechanisms and ontogeny".

Psychobehavioral sex differences ultimately arise from sexual selection, sexual differentiation of the mammalian brain, sexual division of labor, and their interactions (**Figure 1**). Sexual selection and sex differences in parental investment have shaped status-striving and power-seeking among men more than in women, resulting in (sometimes violent) competition, risky economic pursuits, and men taking on more leadership positions than women, particularly at higher organizational and societal levels (Gottschall, 2008; Vongas and Al Hajj, 2015; Sweet-Cushman, 2016; von Rueden et al., 2018; Garfield et al., 2019b; Luoto, 2019, 2020; Welling and Shackelford, 2019; Van Vugt and von Rueden, 2020). The mammalian pattern of inter-male competition arises partially because fertile females are a limiting resource for male reproduction (i.e., the Darwin–Bateman paradigm: see Fromhage and Jennions, 2016; Janicke et al., 2016; Hoquet, 2020; and Morimoto, 2020 for recent discussions), which generally leads to higher risk-taking and status-seeking in males relative to females (Archer, 2019; Ronay et al., 2020). Women's higher empathy and people orientation, in contrast, may be driven by an evolutionarily ancient maternal tendency to care for offspring (Panksepp, 1998; Christov-Moore et al., 2014), interacting with a tend-and-befriend response to psychosocial stress (Nickels et al., 2017; Youssef et al., 2018). Nevertheless, it should be noted that intrasexual rivalry exists also in women (Fisher, 2017), particularly in physical attractiveness and romantic contexts (Rantala et al., 2019; Reynolds, 2021). In the workplace, men and women prefer to compete intrasexually rather than intersexually, but women tend to be more hesitant and calculated in their competitive approach than men (Kocum et al., 2017). Finally, among men, financial success and mating competition/success are correlated—in women, they are uncorrelated (Kocum et al., 2017; see also Luoto, 2019).

While some hold the position that socialization into gender roles causes sex differences in humans, this hypothesis is generally not supported when considering the biological, developmental, neuroscientific, and cross-national evidence more broadly (Christov-Moore et al., 2014; Schmitt, 2015; Janicke et al., 2016; Archer, 2019; Del Giudice, 2019; Luoto et al., 2019a; Liu et al., 2020; Stoet and Geary, 2020). In fact, cross-national evidence indicates that in more gender-egalitarian countries, sex differences are of a higher magnitude than in less gender-egalitarian countries, which is the opposite of what the gender role hypothesis would predict (Schmitt et al., 2008; Falk and Hermle, 2018; Atari et al., 2020; Stoet and Geary, 2020; see also Breda et al., 2020)[9]. Furthermore, since evolutionary processes pre-date social conceptualizations of gender roles by several million years, a complete explanation of the interplay between social conceptions of gender roles and evolved biological predispositions would need to account for how evolutionary processes act as precursors to gender roles (Janicke et al., 2016; Sweet-Cushman, 2016; Archer, 2019).

To bridge this evolutionary approach with the COVID-19 context, there is an important evolutionary aspect behind the hypervigilance, anticipatory anxiety, and threat sensitivity associated with women's higher neuroticism, risk aversion, and fearfulness (Nettle, 2011; Barlow et al., 2014; Archer, 2019). Error Management Theory predicts that when the cost of missing a real threat is greater than seeing an illusion of threat, evolution selects the less costly error (Haselton and Nettle, 2006). In effect, once a person is fearful, less evidence will trigger a threat response—thus, there will be a higher false alarm rate, which protects against the cost of not perceiving a real threat (Tooby and Cosmides, 2008). The strategic shift in thresholds for signal detection experienced by neurotic individuals leads more often to protective false alarms which are essential in dangerous real-life situations, such as the COVID-19 pandemic. Viability selection and sexual selection (Cornwallis and Uller, 2010) might have acted together in selecting for higher threat vigilance in women (i.e., higher neuroticism) given women's relatively much lower strength and thus lower self-defense abilities (Lassek and Gaulin, 2009; Nettle, 2011). Although environments experienced by the sexes do not differ substantially, the impacts of undetected threats can be higher for women because of their lower strength and higher parental investment, which may partially increase selection pressures for women's higher neuroticism, anxiety, and risk aversion (Lassek and Gaulin, 2009; Nettle, 2011). This evolutionary reason of more protective false alarms in women might also be behind women's higher levels of compliance with protective measures (Moran and Del Valle, 2016; Galasso et al., 2020) and behind female leaders' decision to act more quickly during the pandemic (Garikipati and Kambhampati, 2020; though see Aldrich and Lotito, 2020), potentially saving more lives. This female-typical 'false alarm' line of reasoning from Error Management Theory (Haselton and Nettle, 2006) is of crucial importance for public policy-making during pandemics when the threat of the virus can be more effectively curtailed when it is anticipated rather than experienced.

Phylogeny

To provide a comprehensive evolutionary account on sex differences, it is valuable to take a broader view into mammalian sexual differentiation of brain and behavior (Janicke et al., 2016; Lonsdorf, 2017; Luoto et al., 2019a; Arnold, 2020; Liu et al., 2020). Evidence of overt sex−biased treatment by others (equivalent to

[9]Whether similar or opposite patterns are seen in cross-cultural variation in women's motivation to engage in leadership remains to be determined.

what social constructionists think of as socialization into gender roles in humans) is lacking in many species of non-human animals. In the few species that have been studied, little to no difference has been found in behaviors of mothers toward female and male offspring (Lonsdorf, 2017). Nevertheless, such species show sex differences in behavioral development that resemble differences found in infant humans (Christov-Moore et al., 2014; Lonsdorf, 2017; Archer, 2019). These include differences in physical and social development and in species-typical behaviors such as grooming, playing, object manipulation, and extractive foraging (Lonsdorf, 2017). Immature chimpanzee males engaged in more object-oriented play than females (Koops et al., 2015). Newborn rhesus macaque females that were under 5 weeks old and were raised in a controlled postnatal environment looked more at computer-generated faces of other rhesus macaques and engaged in more affiliative behavior with a human caregiver than newborn rhesus macaque males did (Simpson et al., 2016). Likewise in humans: 12-month-old female infants showed a higher relative preference for a moving face over a moving car than males did (d = –0.64) (Lutchmaya and Baron-Cohen, 2002). As in humans, vervet and rhesus monkey females played longer with dolls and plush toys, and males played longer with wheeled toys (Christov-Moore et al., 2014). Asian elephant females tend to be more social and gregarious than males, suggesting that females are more affectionate and seek out others and are sought out by others as company (Seltmann et al., 2019). Human and non-human primate females engage in social grooming more often than males do (Lonsdorf, 2017). In both hamsters and humans, females find same-sex social interactions more rewarding than males do. The finding that oxytocin has a similar mechanistic role in social reward processing in a number of species suggests that sociality and sex differences in sociality may have a deep common evolutionary origin (Feng et al., 2015; Hung et al., 2017; Borland et al., 2018).

An analysis of 76 non-human mammal species (Smith et al., 2020) showed that female-biased leadership manifested most often as females leading collective movements. Of the 76 non-human mammal species, female-biased leadership was reported only in eight species: (1) bonobos (*Pan paniscus*), (2) ring-tailed lemurs (*Lemur catta*), (3) black-and-white ruffed lemurs (*Varecia variegata*), (4) killer whales (*Orcinus orca*), (5) spotted hyenas (*Crocuta crocuta*), (6) African lions (*Panthera leo*), (7) African bush elephants (*Loxodonta africana*), and (8) Asian elephants (*Elephas maximus*). Male-biased leadership therefore is the most typical across the mammalian lineage (Smith et al., 2020), including humans, both in large-scale post-industrial societies as well as more egalitarian, small-scale societies (Garfield et al., 2020).

The closest living relatives of modern humans that have female-biased leadership are bonobos. It has been suggested that same-sex sexual behavior has allowed female bonobos to overcome the phylogenetic legacy of male dominance in primates by "making love, not war" (Smith et al., 2020). Female-biased leadership in bonobos is characterized by peaceful social interactions—and it is common for females to use genital contact to reduce tensions with both males and females (Smith et al., 2020). Leadership in bonobos is therefore non-isomorphic in relation to human leadership. Chimpanzee leadership is male-biased and resembles human leadership more than bonobo leadership does; male chimpanzees, for instance, lead in group hunting, within-group interventions, and intergroup warfare (Smith et al., 2020).

Proximate Mechanisms and Ontogeny

The proximate level of analysis (see e.g., Lewis et al., 2017; Zietsch et al., 2020, for a discussion of the proximate–ultimate distinction) focuses on the biological and/or social mechanisms underlying a trait or behavior. Accumulating evidence indicates that sex hormones play a key role not only in sexual differentiation of the brain (**Figure 1**; Luoto et al., 2019a,b; Arnold, 2020), but also in sexual dimorphism in the activation of the endocannabinoid and the mesocorticolimbic pathways, both of which create sex differences in reward-seeking behaviors. These sex differences, though operating within a continuum, are central in shaping a number of life outcomes from sexual behavior, sensation-seeking, substance use, and risk-taking to variation in health (Struik et al., 2018; Becker et al., 2019; Luoto et al., 2019a,b, 2021; Mauvais-Jarvis et al., 2020).

During critical periods of development in fetal and neonatal life, testicular secretions have permanent effects on the brain, driving sexual differentiation of the brain (Arnold, 2017; Forger, 2018; Kret and De Gelder, 2012; Luoto et al., 2019a,b). There are three major classes of proximate sex-biasing factors: sex chromosome effects (the differential action of X and Y genes or chromatin that are out of balance in XX and XY genomes), and organizational and activational effects of gonadal hormones (Arnold, 2020; see also McCarthy, 2020). Unlike activational effects, the early organizational effects of gonadal hormones are considered irreversible, creating various degrees of masculinized phenotypes in brain, physiology, cognition, and behavior (**Figure 1**; Luoto et al., 2019a,b; Arnold, 2020).

Exposure to androgens has an effect on neuronal survival and connections (Kret and De Gelder, 2012) and can play an important role in the sex-specific development of the endocannabinoid system, which directs reward-related behavior (Struik et al., 2018; Luoto et al., 2019b) and which may therefore partially underlie the psychological sex differences reported above (Luoto et al., 2019a). Testosterone, for instance, has both organizational and activational effects on risk aversion and choosing risky careers in finance (Sapienza et al., 2009; see also Apicella et al., 2015). Individuals with genetic disorders provide additional evidence on the ways in which sex hormones direct development. Congenital adrenal hyperplasia (CAH) is a genetic disorder that affects adrenal glands and results in an overproduction of testosterone in affected women. A study comparing unaffected men and women in people and things orientation reported a very large (d = –2.02) sex difference, with men scoring higher on things orientation and women scoring higher on people orientation (Beltz et al., 2011). Interest in things relative to people was higher in women with CAH than in unaffected women (d = 0.75) as can be predicted by the higher dose of testosterone to which CAH women are exposed (Beltz et al., 2011). People and things orientation was correlated

with the degree of androgen exposure: women with a severe form of CAH had higher scores on things orientation than women with milder forms of CAH. CAH women also reported a higher interest in scientific occupations ($d = 0.56$) and mechanical occupations ($d = 0.64$) but lower interest in social occupations ($d = -0.30$) than their unaffected siblings (Beltz et al., 2011), which highlights the masculinizing effect of testosterone (cf. Luoto et al., 2019a).

While significant differences between men's and women's brains have been reported in adulthood (Del Giudice, 2019), Wheelock et al. (2019) were the first to report the existence of sex differences in the human brain *in utero*. More specifically, Wheelock et al. (2019) reported that functional connectivity of the human brain is organized into highly fragmented prenatal brain networks, and that prenatal functional connectivity varies with regard to fetal sex and gestational age. These findings provide strong evidence against claims about brain sexual differentiation occurring because men and women are differentially socialized into gender roles (Rippon, 2019). Wheelock and colleagues' findings on the prenatal sexual differentiation of the human brain further reinforce biological theories of brain sexual differentiation and core gender identity development (Fisher et al., 2018; Luoto et al., 2019a; Arnold, 2020; McCarthy, 2020). Neurodevelopmental theories of gender identity development are also supported by longitudinal research. While hormone exposure significantly predicted gender development in girls, their mothers' socialization efforts to feminize the daughters had negligible effects: women subjected to more testosterone in prenatal development showed masculinized behaviors in adulthood despite their parents' socialization efforts to make the daughters more feminine (Udry, 2000; see also Luoto et al., 2019a).

Research on the sexual differentiation of the mammalian brain, mirror neurons, theory of mind, and the evolutionary origins of empathy (Christov-Moore et al., 2014; Peterson and Bartels, 2017; Luoto et al., 2019a; Luoto, 2020) suggests that there are biological mechanisms underlying the psychological sex differences reviewed above. Women are better than men at interpreting others' intentions and actions, demonstrating an improved domain-specific ability to read others' minds (Ibanez et al., 2013; Varella, 2018). Psychologically, this sex difference is mediated by empathy (Ibanez et al., 2013), a trait in which sex differences are well known (Archer, 2019). Developmentally, theory of mind is affected by prenatal androgen exposure (Khorashad et al., 2018), which is an important neurodevelopmental mechanism giving rise to many psychobehavioral sex differences (Luoto et al., 2019a,b; Arnold, 2020), including people–things orientation (Beltz et al., 2011; Luoto, 2020). Women have increased mirror neuron activity when evaluating the emotions of others (Peterson and Bartels, 2017), and men and women differ qualitatively in how emotional information is integrated to support decision-making processes (Christov-Moore et al., 2014). In the aggregate, these findings suggest that women may be more empathetic leaders than men (cf. Sergent and Stajkovic, 2020), and that the sexual differentiation of the mammalian brain is one of the main underlying biological processes causing psychobehavioral sex differences in humans (**Figure 1**).

SEXUALLY DIMORPHIC LEADERSHIP SPECIALIZATION HYPOTHESIS

We have collated recent evidence which suggests that female leaders may be more effective than male leaders in a pandemic context, particularly reducing mortality outcomes. We connected this leadership strength with women's evolved sex-typical psychobehavioral traits. Given the stability, universality, and phylogenetic inertia of those sex-typical traits (Geary, 2010; Lonsdorf, 2017; Archer, 2019), it is possible to infer that a similar leadership success of women during disease outbreaks would, for the same sex-typical psychobehavioral characteristics, also have existed during ancestral times, depending also on followers' reactions, contextual factors, and local cultural norms. After all, humans have an evolved leadership psychology (Garfield et al., 2019b; Van Vugt and von Rueden, 2020), and this sex-specificity could be a part of it.

The hypothesis about the possible ancestral effectiveness of female leadership during a disease outbreak complements the literature on the evolved aspects of male political leadership, particularly regarding the different ecological and sociopolitical threats that societies have faced throughout primate evolution (cf. Watts, 2010; McDonald et al., 2012; Smith et al., 2020). Males, on average, engage in more risk-taking and aggressive activities than women, and those sex differences have a long evolutionary history (Van Vugt, 2009; Geary, 2010; Sweet-Cushman, 2016; Archer, 2019). In recent and in ancestral times, intergroup conflicts were frequent and entailed a substantial mortality rate (Bowles, 2009). Formidable and dominant male community leaders would have been preferred particularly in times of intergroup conflict and war (Hayden et al., 1986; Grabo and van Vugt, 2018; Garfield et al., 2019b), which could have resulted in higher reproductive success for the experienced warrior leaders (von Rueden et al., 2011; Glowacki and Wrangham, 2015; von Rueden and Jaeggi, 2016), despite the individual agency of the male leader being less crucial than social networks in between-group violence (Glowacki et al., 2016). Tigue et al. (2012) found that manipulated lower voice pitch of recordings of US presidents was more strongly associated with physical prowess in a wartime voting scenario and that participants preferred to vote for the candidate with the lower-pitched voice, which indicates dominance (Wolff and Puts, 2010; Aung and Puts, 2020). Similar results have been reported in other studies (Little et al., 2007; Halevy et al., 2012; Spisak et al., 2012). Facial cues associated with perceived height and masculinity in potential leaders' faces are valued more in a wartime context vs. peacetime context (Spisak et al., 2012; Re et al., 2013; Grabo and van Vugt, 2018). Preference for leader dominance seems to be uniquely driven by the intuitive notion that dominant leaders are better in giving an aggressive response in times of social conflict (Laustsen and Petersen, 2017). Current evidence suggests that the predominant preference for male over female political leaders could be a byproduct of the ancestral preference for physically formidable

allies (Murray and Carroll, 2020). Furthermore, other aspects of the dominant male leader can also be relevant to the in-group, such as better coordination, negotiation, and efficiency at suppressing free-riding (Lukaszewski et al., 2016; see also Varella et al., 2021; Yong and Choy, 2021).

This male and female leadership differentiation, preference, and effectiveness could be either (1) a byproduct of more general sex differences in physiology, cognition, and behavior (cf. von Rueden et al., 2018; Archer, 2019), or (2) an evolved sex-specific specialization in different kinds of leadership styles. We refer to this second alternative as the *sexually dimorphic leadership specialization hypothesis*. According to this hypothesis, it would have been more effective to have male community leaders during ancestral (and recent) times of frequent wars, aggression (both intergroup and intragroup), and possibly during geological and other natural hazards, while during disease outbreaks and famines it would have been more effective to have female leaders. This possible sex-specific specialization would result from the coevolution between male and female roles as leaders in which men's and women's psychological strengths were recurrently recruited by society and/or followers and used for leadership in different and correspondent threat contexts based on the effectiveness of leadership outcomes in each context. This hypothesis can also be extended to coalitions of leaders; those coalitions with a higher proportion of males would deal better with violent conflicts, while those with a higher proportion of females would deal better with epidemics.

Although there are interrelationships among all classes of environmental threats, they do not always appear simultaneously nor with the same frequency. Infectious disease outbreaks increase ethnocentrism and resource scarcity which later tend to lead to armed conflict and civil wars (Letendre et al., 2010). Conversely, times of war and conflict tend to contribute to pandemic outbreaks (Habicht et al., 2020). However, many more factors trigger conflicts, such as increases in temperature or in extreme rainfall (Hsiang et al., 2013; see also Van Lange et al., 2017), or social/economic inequalities (Stewart et al., 2002), than disease outbreaks, so much so that violent conflicts are much more frequent (Stewart et al., 2002; Letendre et al., 2010; Hsiang et al., 2013) than epidemics and pandemics (Hays, 2005; Habicht et al., 2020). Hence, this disparity creates differential selective pressures on leadership which underliers the sexually dimorphic leadership specialization hypothesis and, consequently, the observed higher prevalence of male leadership.

The premise of this hypothesis is the idea that sexually dimorphic leadership specialization is an *exaptation*, as it hypothetically arose from sexually dimorphic psychological traits which evolved for other purposes, such as higher status-seeking, particularly in high-level organizational contexts, as well as male–male aggression in men—and maternal care, empathizing, and pathogen disgust in women (e.g., Geary, 2010; Archer, 2019). An exaptation is a feature that improves fitness in a way that differs from its "original" evolutionarily selected role, having acquired a novel function in the course of evolution (Gould and Vrba, 1982; Gould, 1991; Buss et al., 1998; Luoto, 2019). A correspondent and consequent new phenomenon stemming from this process of exaptation would be a context-specific preference for leaders of each sex.

The evidence we have reviewed suggests this might be the case with sexually dimorphic leadership specialization, though it would be necessary to establish the kinds of fitness benefits (and costs) that women accrue from positions of leadership (cf. Sweet-Cushman, 2016; Garfield et al., 2020). There is existing research on the fitness benefits of leadership for male leaders, namely more in-pair surviving offspring as well as more extra-marital affairs and higher wife quality (von Rueden et al., 2011; von Rueden and Jaeggi, 2016; Spisak, 2020). A study using ethnographic records from 60 cultures showed that male leaders tend to be more polygynous than non-leaders across cultures (Garfield et al., 2019a).

As such, the sexually dimorphic leadership specialization hypothesis is consistent with how sex differences in parental investment and mating competition coevolve with parental care specialization, based partially on ecological factors (Henshaw et al., 2019). Evolutionarily, parental investment consists of two or more distinct activities: provisioning and defense. Consequently, parents may care more efficiently if they specialize in a subset of these activities when it is inefficient for a single parent to provide multiple types of care (Henshaw et al., 2019). This kind of parental care specialization occurs in many taxa (Janicke et al., 2016; Henshaw et al., 2019). Based on what is known on psychobehavioral sex differences and their evolution in humans, the sexually dimorphic leadership specialization hypothesis extends (**Figure 1**) models on the evolution of parental care specialization (Trivers, 1972; Janicke et al., 2016; Henshaw et al., 2019)—and the biological constraints of parental care on economic activity (Starkweather et al., 2020)—to leadership types.

Nevertheless, more work is required to address the question of fitness benefits and costs of leadership in women. It is highly likely that men and women differ with regard to the fitness-related benefits and costs associated with positions of leadership—and that this difference is caused and/or mediated by sex differences in (1) parental investment, (2) age-related fertility decline, (3) mate preferences, (4) reproductive physiology, (5) reproductive ecology, and (6) sexual and reproductive decision-making (Trivers, 1972; Valeggia and Núñez-de la Mora, 2015; Sweet-Cushman, 2016; García et al., 2018; Archer, 2019; Buss and Schmitt, 2019; Luoto, 2019; Hughes et al., 2021). Evolutionary theory supports the view that men are able to derive significant reproductive benefits from politically ambitious behavior, while fewer benefits accrue to women from similar behaviors (Sweet-Cushman, 2016; see also von Rueden et al., 2011; Buss and Schmitt, 2019; Garfield et al., 2020). Women who try to use resources and status to attract multiple mates are not distinctly favored by natural selection, whereas men are (Geary, 2010; von Rueden et al., 2011; Sweet-Cushman, 2016; Luoto, 2019)[10]. However, politically influential women may be able to bear healthier offspring (Alami et al., 2020), possibly because of higher resource availability which supports somatic and immunological development (cf. Krams et al., 2019; Rubika et al., 2020). Moreover, in a hunter-gatherer society, male and female leaders

[10]Traits other than resources and status may be more beneficial for women when acquiring extra-pair matings.

share a similar phenotypic profile and are rated as having higher spouse quality than non-leaders; thus, they tend to be married to one another (von Rueden et al., 2018; Garfield and Hagen, 2020), which might improve offspring quality and social status[11].

An evolutionary approach to leadership recognizes that ancestrally there may have been limited incentive for women to take the risks associated with gaining and holding on to power in the public sphere, which partially explains sex differences in leadership prevalence and political ambitions (Sweet-Cushman, 2016; cf. Garfield et al., 2020; Smith et al., 2020). Nevertheless, it is possible that if leadership is analyzed on different levels of social organization (e.g., within and between families), men and women could show different leadership pattern on different levels—women up to the extended family level, men at higher organizational and societal levels—to the extent that if taking family leadership into account, the overall sex difference in leadership could diminish, vanish, or even reverse, favoring females (Garfield et al., 2019a). Cross-nationally, men's status hinges more on athleticism, bravery, physical formidability, hunting skills, and aspects of leadership, while women's status is more dependent on physical attractiveness and domestic skills (e.g., processing food, childcare) (Buss et al., 2020). Female leaders in horticultural and hunter-gatherer societies were more likely than male leaders to be in a polygynous marriage with a high-quality spouse, to receive *more* social, reproductive, and material success whilst having *less* prosocial competence than male leaders (Garfield et al., 2020). These surprising results suggest that female leaders tend to be high-status wives who gain social influence across the lifespan through their high-quality polygynous spouse, extended kin, and social networks (Garfield et al., 2020); however, because of the exploratory nature of this study, as well as the small sample size of female leaders, these findings await further confirmation.

Notably, the sexually dimorphic leadership specialization hypothesis does not suggest that effective leadership is exclusive to either males or females, nor that half of the time each sex would be in charge as a leader; rather, it posits that, on average, evolved predispositions would bias men's and women's leadership styles to focus relatively more on different areas (intergroup aggression vs. health and societal care) which become prominent during different contexts.

ASSESSING THE EVIDENCE FOR THE SEXUALLY DIMORPHIC LEADERSHIP SPECIALIZATION HYPOTHESIS

Despite the lack of direct systematic evidence on the sexually dimorphic leadership specialization hypothesis, it is supported by circumstantial evidence stemming from diverse sources from hunter-gatherers to large-scale post-industrial societies, which we touched on above and review in more detail below. We should in any case note that the fact that female leadership is phylogenetically far less prevalent than male leadership and shows phylogenetic inertia in the mammalian lineage (Smith et al., 2020) could be tentatively interpreted as evidence against the sexually dimorphic leadership specialization hypothesis, seeing that the kinds of contexts which the hypothesis posits will select for female leadership (disease outbreaks, famines) were sporadic but recurring threats both evolutionarily and in recent history. We therefore do not rule out the hypothesis that sex differences in leadership are merely a coincidental byproduct of more general psychological sex differences which evolved for purposes other than leadership.

Before we review evidence for the sexually dimorphic leadership specialization hypothesis, we also note that there is some evidence against it. A study on sex differences in state leadership in Europe between 1480 and 1913 reported that queens engaged more in wars in which their polity was the aggressor than kings did (Dube and Harish, 2020). However, this effect varied by marital status. Unmarried queens were attacked more than kings. Among married monarchs, queens acted as attackers more than kings. The results suggest that unmarried queens may have been attacked because they were perceived to be weak, while married queens may have had greater capacity to attack supported by their spouses who helped them rule (Dube and Harish, 2020). Furthermore, if queens tended to lose wars more than kings, it would provide evidence in favor of the sexually dimorphic leadership specialization hypothesis, which posits that males are more effective leaders in a wartime context. Evidence at this high level may be subject to complex modifiers, which is why evidence of effectiveness of female leaders during war vs. pandemics may be propitiously analyzed at smaller social scales.

Given the stability, universality, and phylogenetic continuity of the relevant sex-typical traits (Geary, 2010; Lonsdorf, 2017; Falk and Hermle, 2018; Archer, 2019) in which sex-differences in leadership are presumably based (Sweet-Cushman, 2016; Garfield et al., 2019b; Smith et al., 2020), convergent evidence from hunter-gatherers and large-scale post-industrial societies tends to support the sexually dimorphic leadership specialization hypothesis. However, besides the current pandemic, there is a lack of systematic evidence related to sex-dependent effectiveness of leadership during public health crises (cf. Knebel et al., 2012). There are some selected historical cases that arguably could point to where future systematic studies could be conducted to test the hypothesis. There are historical examples of female Native American leaders who saved lives by connecting tribal affairs and public health programs against contagious diseases, such as tuberculosis (Trennert, 1998; Davies, 2001). Of all indigenous female roles, few are as notable as the medicine woman/traditional healer (Lajimodiere, 2013; Mji, 2019). There are scattered historical examples of women nurses providing significant leadership in healthcare crisis response (Schoch-Spana, 2001; Bristow, 2012; Knebel et al., 2012; Patterson, 2012; Fawole et al., 2016), although there are also some instances of male nurse leadership (Evans, 2004). During the foot-and-mouth disease and the bovine spongiform encephalopathy crisis (1990s–2000s), there was a contrast between the disorganized and slow UK response led by males and the rapid and effective

[11] A limitation of these findings is that the women who were coded as leaders in that study did not necessarily have a formal leadership position, but may have gained their influence because of their marriage to a high-status male (Garfield and Hagen, 2020), making it difficult to ascertain the direction of causality between their influence and marital status.

French response led mostly by females (Kahn, 2020). Moreover, women have led initiatives developing response, relief, and recovery measures from many past disasters, such as hurricanes and disease outbreaks (Enarson, 2012, p. 245). We do not claim that these instances are an extensive literature review nor that they systematically test the sexually dimorphic leadership specialization hypothesis, only that together they can offer an initial and possible pattern in that direction, which should guide future systematic analyses on sex differences in leadership during disease outbreaks.

Neuroscientific evidence points to distinct and antagonistic brain areas related to two leadership roles: the task-oriented leadership role is attributed to activation of the task-positive network, while the socio-emotionally oriented leadership role relies more on the default mode network (Boyatzis et al., 2014). These brain specializations and mutual suppression of activities related to different leadership styles might be the neurobiological basis for sexually dimorphic specialization in leadership. There are even genetic specificities of each leadership style: additive heritability (the effect of multiple genes that exert influence in a linear or additive fashion) is more related to transactional leadership style, while non-additive heritability (interactive effects of different alleles: within-locus dominance and across-locus epistasis) is more related to transformational leadership style (Johnson et al., 1998). Importantly, these leadership roles show a sex difference (Peterson and Bartels, 2017). The task-oriented role of leadership is related to the inflexible "staying the course" of male leadership style and its autocratic dimension, while the socio-emotionally oriented role matches the more intuitive, sensitive, empathetic, and democratic leadership styles of women (Eagly and Johnson, 1990; Peterson and Bartels, 2017). Moreover, men, on average, tend to prefer power, resources, and being feared, while women tend to prefer status, being respected, and loved (Hays, 2013). Such overall patterns in leadership are consistent with the sex-typical psychobehavioral strengths of women with regard to empathy, people orientation, care and health orientation, emotional expression, and sense of fairness and purity—and of men with regard to risk-taking, competitiveness, systemizing, the Dark Triad traits, physical aggression, violence, pain tolerance, and lack of fearfulness, shame, and guilt (Geary, 2010; Varella et al., 2016; Archer, 2019; Atari et al., 2020; Luoto, 2020; Prichard and Christman, 2020).

Evidence from occupational choices shows that homemaking (94% women), administration (75%), and healthcare (70%) are the top three careers with high proportion of women—and importantly, those occupations require the highest empathizing-biased cognitive style (Manning et al., 2010) as well as people orientation (Tay et al., 2019). In contrast, professions such as general management and government/military (both 64% men) and business development (62% men) favor individuals with higher systemizing cognitive styles (Manning et al., 2010; see also Luoto, 2020). Similar patterns are found in academic publishing. Nursing and health professions favor empathizing cognitive styles and a strong people orientation, and they have a high degree of female researchers/authors. Academic fields with strong systemizing requirements and a high things orientation, including economics, tend to have a much higher proportion of male researchers as authors (Luoto, 2020). A study on 22 established democracies between 1970 and 2000 reported that an increased proportion of women in the legislature decreased defense spending and conflict behavior, even after controlling for government partisanship and the rights of women in society (Koch and Fulton, 2011). Other research on policymaking has reported significant sex differences in implementing policies related to health, development aid, the environment, defense spending, women's issues, and welfare policy (Hessami and da Fonseca, 2020). The evolved sex-typical psychobehavioral strengths may lead to these distinctions of policymaking and vocational choice, whilst also predisposing leaders to use their talents and strengths in the respective leadership contexts predicted by the sexually dimorphic leadership specialization hypothesis: women focusing more on healthcare, welfare, and society, and men focusing more on intergroup aggression, military, and the economy.

The hunter-gatherer socio-ecological way of life resembles the social structure and functioning of ancestral human lifestyles during the Pleistocene, and is thus informative with regard to *Homo sapiens* evolutionary history (e.g., Sweet-Cushman, 2016; though see Moreau, 2020). Male leaders across 59 mostly non-industrial populations had higher military command and distributed resources more often than female leaders did (Supplementary Figure S12 in Garfield et al., 2020). Anthropological evidence from egalitarian small-scale societies suggests that leadership emerges facultatively according to context-specific demands in serving the collective interests rather than from a single powerful authoritative figure (Garfield et al., 2019b). Human leaders tend to lead in one or a few domains, and there are usually many concomitant leaders in different areas such as hunting, group defense, and traditional healing (e.g., shamans) (Garfield et al., 2019b). It is probable that humankind's earliest politicians, headmen, were exclusively men (Sweet-Cushman, 2016). Although shamans and traditional healers can be either male or female and the empirical evidence is ambiguous about it in small-scale societies (e.g., Brown et al., 2006; Jaradat and Zaid, 2019; Audet et al., 2020), the healing practices of shamans (Garfield et al., 2020), particularly involving trance performances of 'spirit' possession, are often done by women in larger and more hierarchically layered societies (Wood and Stockly, 2018). There are even cases in which males change their gender roles by dressing and behaving in feminine ways to be able to practice shamanism (Tomášková, 2013). At least 10% of non-industrial societies have women in leadership positions, and in some instances shamans are also considered leaders (Garfield et al., 2019b).

An evolutionary view of leadership across species and societies has identified two main widespread types of leadership: one based on physical and social formidability (dominance), and another based on information and skills (prestige) (Garfield et al., 2019b; Van Vugt and von Rueden, 2020). This framework is consistent with empirical evidence showing that there are two distinct and viable routes to ascend in social rank: dominance (use of force and intimidation to induce fear, and selfishly manipulating the group resources) and prestige (sharing of expertise/valued knowledge or know-how to gain respect) (cf. Cheng et al.,

2013; Maner and Case, 2016). Although the same leader can make use of both types of strategies, the evolved sex-typical psychobehavioral tendencies influencing leadership may incline male leaders to rely on the dominance strategy more often (cf. Evans, 2004) and female leaders to more frequently use the prestige strategy (cf. Holmgren et al., 2019). Indeed, female leaders in a forager-horticulturalists society in Ethiopia showed high prestige but low dominance, whereas male leaders were high on both prestige and dominance (Garfield and Hagen, 2020). We predict that this sexual dimorphism in leadership styles becomes more accentuated under distinct threat contexts (e.g., intergroup conflict vs. disease outbreaks). Such sex-specific responses to threats would be in line with the female-typical 'tend-and-befriend' response and the male-typical 'fight or flight' response to psycho-physiological stress (cf. Nickels et al., 2017).

Organizational literature on modern company leaders also points in the same direction as the above evidence. Women tend to be mostly chosen to lead whenever an organizational crisis is minimal to moderate and stems primarily from within the organization, while men tend to be chosen as leaders whenever the crisis threatens the very existence of the organization and its source is an external threat (Vongas and Al Hajj, 2015). Although within-group threats such as free-riding and crimes from other group members also increase preference for dominant-looking leaders (Bøggild and Laustsen, 2016) or those described verbally as dominant (Zhu et al., 2021), female leaders are preferred for the resolution of within-group disputes while male leaders are preferred to lead under conditions of intergroup conflict (Van Vugt and Spisak, 2008). As any microscopic pathogenic agent enters the group and slowly contaminates in-group members, it constitutes a within-group crisis. Hence, according to this literature, it is more probable that women would be assigned to lead the group out of this kind of pathogen-induced threat, in accordance with the sexually dimorphic leadership specialization hypothesis. The hypothesis is also consistent (though not fully overlapping) with evidence indicating that human and non-human animal leaders are often chosen based not necessarily on sex, but on the attributes that signal their competence to lead group activities (Smith et al., 2020; see also Garfield et al., 2020).

By introducing this hypothesis, we aim to highlight this pattern of sex specialization in leadership and point to possible avenues for future research. The sexually dimorphic leadership specialization hypothesis, which posits that the balance of male/female leadership shifts depending on the context of the main threat to the group, is not offered as a mere 'just so story' (cf. Varella et al., 2013). Instead, we have provided deeper insights based on the patterns observed in existing literature from various fields, and invite further testing by offering convergent circumstantial evidence for the hypothesis. These future studies would thus go beyond the 'null hypothesis' of seeing women's leadership success during the COVID-19 pandemic merely as a recent byproduct of evolved sex differences, which only now happen to manifest in a leadership context. The sexually dimorphic leadership specialization hypothesis could be further tested by studying the sex-specific fitness benefits and costs associated with leadership (cf. Garfield et al., 2020; Spisak, 2020), as well as details on how a population's socioecological and cultural contexts influence the type of preferred leader.

Based on the sexually dimorphic leadership specialization hypothesis, it can be predicted that women, feminine individuals, or female-biased or feminine coalitions would be more motivated to help save lives during disease outbreaks, leading more effective societal responses, particularly in less patriarchal, more gender-egalitarian societies where women have unobstructed access to the political sphere. In small-scale societies, anthropologists can study sex differences in leadership during disease outbreaks, while historians are encouraged to focus on sex differences in formal (elected) or informal (e.g., head nurses) leadership during past disease outbreaks. In lab experiments, participants primed with pandemic (versus war-time) contexts are predicted to positively evaluate, vote for, or trust in feminine (versus masculine) political candidate faces/voices. Both manifest protective/caretaking behaviors during disease outbreaks and psychological tendencies/bias toward protection/caretaking should be empirically assessed in studies on female vs. male leaders.

DISCUSSION

Evolutionary science has been applied to understanding and predicting specific outcomes of the COVID-19 pandemic in various ways (Arnot et al., 2020; Corpuz et al., 2020; Seitz et al., 2020; Varella et al., 2021). However, sex differences in pandemic leadership have not been previously approached from an evolutionary perspective. As such, an evolutionary approach offers an alternative explanation to other hypotheses on sex differences in leadership and policymaking. In fact, a prominent theoretical position in the political economy literature suggests that personal characteristics of officeholders do not matter for policy choices, yet empirical evidence reviewed here and elsewhere does not support this hypothesis (Hessami and da Fonseca, 2020).

A convergence of key findings strengthens the case for an evolutionary approach to leadership in general, and manifest sex differences in leadership behaviors in particular. Leadership is universal among industrial and small-scale societies, including hunter-gatherers (Zagorsek, 2004; Price and Van Vugt, 2014; Garfield et al., 2019b). Possible universal traits of leaders include qualities such as being knowledgeable, intelligent, and capable in conflict resolution (Garfield et al., 2020). There are clear shared phylogenetic (among big carnivores, great apes, and extinct hominids) and ontogenetic (among children, adolescents, and adults) patterns of leadership (Garfield et al., 2019b). Propensity for leadership is heritable, with an estimated genetic contribution of 44% in women and 37% in men (Chaturvedi et al., 2012). A specific genotype is associated with the tendency to occupy a leadership position (De Neve et al., 2013). There are specific neural networks underlying differentiated leadership types (Boyatzis et al., 2014; Peterson and Bartels, 2017), and a specific set of cognitive skills utilized in leadership (Mumford et al., 2017). There are sex differences in leadership styles (Peterson and Bartels, 2017; Garfield et al., 2019b), and evidence for differential reproduction in male leaders of small scale hunter-gatherer societies (e.g., polygyny among leaders and monogamy among followers) (von Rueden et al., 2011; Garfield

et al., 2019b), which suggests that sexual selection drives these differences. Leadership has the important evolutionary and social function of instrumentally solving collective action dilemmas while balancing the interests of leaders and followers according to reciprocal altruism and kin selection (von Rueden et al., 2014). All this points to the possible evolved status of the tendency toward leadership in humans: an evolved leadership psychology (Van Vugt and Kurzban, 2011; Sweet-Cushman, 2016; Garfield et al., 2019b; Van Vugt and von Rueden, 2020).

In light of the individual variation within each sex, which tends to be larger than variation between the sexes (e.g., Archer, 2019; Del Giudice, 2019; Landry et al., 2019; Luoto et al., 2019a,b), future studies should analyze whether there are intrasexual differences on masculinity–femininity continuum that mirror the sexually dimorphic tendency in leadership efficacy. After all, cues of masculinity–femininity can be more influential than actual sex cues at predicting perceptions of leadership (Spisak et al., 2012). In this light, our review and hypothesis can be better understood in a more nuanced fashion and focused on maleness and femaleness rather than simply presenting a male vs. female dichotomy (cf. the phenotypic continua in **Figure 1**).

LIMITATIONS

This review has some limitations, as there is still a shortage of empirical studies on many fronts, particularly in a pandemic leadership context. One obvious area for further study would be to analyze political leaders' personality traits, particularly with regard to the psychological sex differences reviewed in this article, using the general population as a reference sample (cf. Wille et al., 2018). Furthermore, some female leaders, such as Jacinda Ardern of New Zealand, have also been praised for their communication skills, which is consistent with the general pattern of higher verbal skills and language ability in women relative to men (Archer, 2019); however, few studies have been conducted on sex differences in communication and language use in a pandemic leadership context (though see Sergent and Stajkovic, 2020; Dada et al., 2021). Another limitation inherent in an evolutionary approach to leadership is the challenge of studying patterns of leadership in extinct hominin species because relevant findings cannot be extracted from fossil records alone, beyond what is possible to infer using body size sexual dimorphism. The fact that we have stressed biological, evolutionary, and mostly dispositional psychological facets does not exclude the possibility that other factors, some of which are contextual or cultural traditions (cf. Hewlett and Hewlett, 2007), might also contribute to female leaders' success during the pandemic, such as reliance on scientific recommendations, consistent public communication about the safety measures, emphasis on uniting the country, the composition of the entire political team, the dominant political ideology of the country, and the leader's educational, personal, and political backgrounds, among others (e.g., Luoto, 2020; Stoet and Geary, 2020).

For instance, to the extent that female politicians are chosen relatively more often to represent liberal political parties and have more liberal values themselves (e.g., Pratto et al., 1997; Oniszczenko et al., 2011; Harteveld et al., 2019), their decisions may reflect liberal values such as equality, social change, and system reform, rather than conservative hierarchic economic values (cf. Oniszczenko et al., 2011; Claessens et al., 2020; Hessami and da Fonseca, 2020). Therefore, studies on sex differences in pandemic leadership should analyze the extent to which political party affiliation mediates the relationship between leaders' sex, the policies they implement, and pandemic-related outcomes. We note that the two national-level studies reviewed in this article did not analyze how leaders' political party affiliations might act as a mediating variable (Garikipati and Kambhampati, 2020; Purkayastha et al., 2020), while the state-level study used political affiliation as a control variable (Sergent and Stajkovic, 2020). We suggest that rather than treating political affiliation as a "nuisance" variable that needs to be controlled for, it might be better conceptualized as a statistical (and theoretical) mediator (cf. Harteveld et al., 2019; Luoto and Jonason, 2019).

Moreover, Garikipati and Kambhampati's (2020) comparison between women- and men-led countries was done without differentiating whether each female leader was a governing leader (such as a prime minister: head of government) or serving in more of a titular role (such as a president: head of state). This analytical decision yields higher statistical power but may obfuscate some of the results based on who were the most influential decision-makers behind pandemic policies (cf. Baekkeskov and Rubin, 2014), with titular leaders having potentially less direct influence on pandemic policy-making than governing leaders.

More generally, the non-randomized assignment of women to political positions constitutes a complex empirical challenge (Hessami and da Fonseca, 2020; Windsor et al., 2020), which is why a multidisciplinary broad-perspective approach, as applied in this article, can best address the complexities of observed sex differences in leadership behaviors and their outcomes. A related potential limitation is that executive positions can have a homogenizing effect on personality and that psychologically more male-typical women may be more likely to pursue and to be chosen for leadership positions (Wille et al., 2018). This may lead to range restriction, a process in which the subjects of a sample are (directly or indirectly) selected from the original population on the basis of their idiosyncratic personal characteristics and therefore do not represent a random sampling of the population (Del Giudice, 2019). It may therefore not be possible to directly extrapolate these findings on leaders to the respective groups of all non-leader women or all non-leader men (or vice versa, for that matter) because only a small subset of each of these groups is likely to become leaders. This limitation can be mitigated by comparing findings on leaders with existing findings on similar group differences from non-leader samples. Thus, to the extent that the findings on leaders are consistent with the findings of other sex difference studies (which they generally tended to be), the sampling problem and range restriction of focusing only on leaders is mitigated.

The fact that we stressed sex differences does not mean that there is no individual variation within the sexes, overlaps between the sexes, or individual plasticity (cf. Bateson and Gluckman, 2011; Del Giudice, 2019; Garfield et al., 2020). It also does not justify or prescribe unequal treatment between

the sexes. It is possible that when men and women work together, they can form stronger teams by combining their specific skills, perspectives, and psychological strengths (e.g., Kruger, 2008; Hessami and da Fonseca, 2020). Both men and women are able to learn from each other's respective leadership styles, thereby broadening their leadership repertoires (Appelbaum et al., 2003; Garfield et al., 2019b). What is more, despite the relative phylogenetic inertia in mammalian leadership patterns, it is also possible that humans can "rise above" their biological history and create social conditions which favor meritocratic leadership regardless of sex (cf. Smith et al., 2020), although gender-based quotas *per se* are likely to have several counterproductive consequences in some contexts. These can include such quota-driven outcomes as creating tension, fostering resentment, impeding collaborative activities, increasing processes of social categorization, intergroup biasing, and competition, being perceived as unfair, bereaving those elected by quotas of their legitimacy and the recognition of their own achievements (Madison, 2019; Euchner and Frech, 2020), and sometimes even adversely affecting collective performance (Yang et al., 2019; though see Liu et al., 2014).

CONCLUSION

Evolutionary science—coupled with a recognition of the proximate neurodevelopmental mechanisms and psychobehavioral predispositions reviewed above—has considerable integrative power in explaining sex differences in and out of politics during a pandemic (**Figure 1**). The research synthesis provided in this article can foster new biopsychosocial research on the ways in which men and women differ in crisis leadership, which psychobehavioral traits those leadership differences are based on, and how the differences can be facultatively harnessed in different ecological and sociopolitical contexts to potentially benefit whole societies. Current evidence indicates that against the invisible viral foe that can bring nations to their knees, the strategies of feminine care-takers and health "worriers" rather than those of masculine risk-taking "warriors" may bring more effective and humanitarian outcomes. We hope that the evolutionary–developmental approach presented in this article contributes to the scientific understanding of sex differences in leadership, inspiring broader consilience across evolutionary science, psychology, political science, anthropology, and developmental, cognitive, and behavioral neuroscience.

AUTHOR CONTRIBUTIONS

SL drafted the manuscript and prepared the data visualization and all Figures. MV reviewed the manuscript critically for intellectual content and conceptualized the sexually dimorphic leadership specialization hypothesis. SL and MV wrote, revised, and approved the final manuscript. Both authors contributed to the article and approved the submitted version.

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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.2021.633862/full#supplementary-material

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Noncompliance With Safety Guidelines as a Free-Riding Strategy: An Evolutionary Game-Theoretic Approach to Cooperation During the COVID-19 Pandemic

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Evolutionary game theory and public goods games offer an important framework to understand cooperation during pandemics. From this perspective, the COVID-19 situation can be conceptualized as a dilemma where people who neglect safety precautions act as free riders, because they get to enjoy the benefits of decreased health risk from others' compliance with policies despite not contributing to or even undermining public safety themselves. At the same time, humans appear to carry a suite of evolved psychological mechanisms aimed at curbing free riding in order to ensure the continued provision of public goods, which can be leveraged to develop more effective measures to promote compliance with regulations. We also highlight factors beyond free riding that reduce compliance rates, such as the emergence of conspiratorial thinking, which seriously undermine the effectiveness of measures to suppress free riding. Together, the current paper outlines the social dynamics that occur in public goods dilemmas involving the spread of infectious disease, highlights the utility and limits of evolutionary game-theoretic approaches for COVID-19 management, and suggests novel directions based on emerging challenges to cooperation.

Keywords: evolutionary game theory, decision-making, COVID-19, free riding, evolutionary psychology, cooperation, public goods, public goods dilemma

INTRODUCTION

The numerous articles on COVID-19 to date represent an impressive effort to come to terms with, inform about, and manage the crisis. We suggest that evolutionary game theory (EGT) and, more specifically, the public goods perspective can significantly add to this discussion and enhance our understanding of human behavior during a global pandemic. From this

perspective, people who disregard safety procedures, such as wearing masks and maintaining social distance, can be understood as free riders because they get to enjoy the benefits of communal safety despite not doing their part to uphold it (Cato et al., 2020). Indeed, there have been calls for more studies on free riding to make sense of uncooperative behavior during COVID-19 (Naso, 2020, p. 72), not least because "continued noncompliance eventually will degrade any benefit associated with these [safety] practices." Such behaviors also do injustice "especially to high-risk groups, people with diseases, and the health workforce trying to treat these patient groups and save their lives" (Paakkari and Okan, 2020, p. e249). As such, the current paper aims to introduce the broader ideas of EGT, describe free-riding behavior in the context of COVID-19, and outline possible mechanisms that may inhibit them. We also consider factors beyond free riding that reduce compliance rates, such as socioeconomic inequality and the emerging problem of conspiracy theory-driven noncooperation that appears immune to free-rider suppression mechanisms. In so doing, we broaden the accessibility of EGT to a wider audience, highlight the utility and limits of EGT for COVID-19 research, and encourage more work in this important area.

EVOLUTIONARY GAME THEORY AND PANDEMICS

Game theory provides a framework to understand strategic decision-making under interdependent payoff structures known as "games" in which a player's outcomes depend on the decisions of other players. The "public goods game" is one such well-studied game-theoretic scenario that affords an examination of people's motivations to partake in the maintenance of public goods, or commodities and services that are available to all members of a society (Olson, 1965; Hardin, 1968). The optimal solution occurs when everyone equally contributes to the provisioning of public goods. However, there are two ways that free riding – or the exploitation of others' cooperation to avoid cooperating – may arise (Apesteguia and Maier-Rigaud, 2006). When the maintenance of a public good (e.g., a clean shared bathroom) depends on the voluntary contributions of a critical number of individuals, an incentive exists for people to avoid bearing those costs when there are sufficient people already contributing, because those who do not contribute are seldom excluded from the benefits. Another form of free riding can occur when public goods are "common pool resources" with a carrying capacity (e.g., a fruit garden). As consumption of resources beyond the carrying capacity limit can lead to rapid depletion of the stock, people are incentivized to take more than a fair share. Yet, if too many people engage in such free-riding behaviors, the sustainability of the public good will be undermined to the detriment of all. Such situations characterize the public goods dilemma, where individuals choose between cooperating to maintain the public good at some personal cost versus free riding if there are already enough cooperative group members. Game-theoretic models indicate that even if individuals are initially cooperative, the inability to exclude free riders renders cooperation an unviable long-term strategy (Perc et al., 2017). Experiments have further confirmed that a lack of measures to suppress free riding pushes individuals toward noncooperation over time (e.g., Fehr and Gächter, 2000; Herrmann et al., 2008; Ibuka et al., 2014).

EGT applies game-theoretic models to biological populations to determine the strategies that evolved for organisms to maximize payoffs in fitness terms (i.e., survival and reproduction; Maynard Smith and Price, 1973; Tooby et al., 2006). Through modeling public goods games, two key adaptive strategies have been identified. On the one hand, humans may have evolved a proclivity to free ride due to the high fitness payoff of selfishness when public goods are available and costs on noncooperative behavior are low. On the other hand, as there are considerable benefits associated with public goods being available, humans also may have evolved psychological adaptations that are geared toward suppressing free riding to facilitate the continued provision of such goods (Tooby et al., 2006). These dynamics can be extended to not only explain difficulties behind real-world scenarios, including voting, law enforcement, and environmental behavior, but also derive solutions that take into account our evolved human nature (e.g., Fehr and Gächter, 2000; Tooby et al., 2006; Bowles and Gintis, 2011; Li et al., 2020).

EGT has also been used to examine the social tensions that occur when a public goods dilemma arises in circumstances involving infectious disease. According to the theory, "herd immunity" emerges when a large enough number of people get vaccinated, which effectively slows and eventually stops the spread of infections (cf. "vaccination game," Fu et al., 2011).[1] As herd immunity becomes a public good, the following social dilemma arises: people can choose between getting vaccinated and contributing to herd immunity versus not getting vaccinated and still benefitting from herd immunity. Because cooperation contributes to the collective benefit of the group at some individual cost (e.g., the hassle or expense of getting vaccinated and potential side effects), whereas a free-riding strategy maximizes individual benefits at no cost (i.e., escaping infection without vaccinating oneself), an incentive to avoid vaccination exists. Experiments indeed show that as a population's vaccination rate increased, people increasingly decided not to vaccinate themselves (Ibuka et al., 2014). The vaccination game also reveals asymmetries in free-riding incentives and risks at different levels of analysis. For instance, the incentive to free ride varies as a function of age as older people are more susceptible to disease compared to younger individuals (Piraveenan et al., 2020). Despite vaccinations being free, quick, and well tolerated by recipients

[1]It is important to note that herd immunity may be elusive or even impossible to achieve with COVID-19 because of the peculiar nature of the SARS-CoV-2 virus, including its various mutations and the propensity for reinfection (Iwasaki, 2021; Sridhar and Gurdasani, 2021; van Oosterhout et al., 2021). Hence, while this section discusses pandemic situations in general, unique features of the SARS-CoV-2 virus may render some of the traditional insights of EGT less applicable to the COVID-19 pandemic.

in developed countries, the urge to free ride can strongly emerge in such populations as they tend to have lower viral prevalence and higher rates of vaccination compared to less developed countries (Sharma et al., 2019).[2] At the same time, our highly globalized world entails that the vulnerability of richer nations hinges critically on the ability of poorer nations with less developed immunization programs to achieve herd immunity (Bollyky and Bown, 2021).[3]

While free riding can emerge as a dominant strategy in the vaccination game, it can also be mitigated in various ways. For example, the isolation of infectious persons and the quarantine of exposed persons can be instrumental in managing the spread of disease, especially when these measures are used jointly (Alam et al., 2020). Another suggestion is to lower the costs or increase the payoffs of cooperation through subsidies and incentive-based vaccination programs (Vardavas et al., 2007), though this approach appears to be effective only or especially under certain conditions, such as when group-based rather than individual-based incentives are used (Chapman et al., 2012), subsidies are targeted at appropriate subpopulations (Ding et al., 2018), vaccine efficacy is sufficiently high (Arefin et al., 2019), and/or information about the status of an infectious disease is publicly available (Ruan et al., 2012). Characteristics of social networks (e.g., heterogeneity) in the population (Kuga and Tanimoto, 2018), which play an important role in influencing the success of cooperative strategies, can also be exploited to enhance the effectiveness of measures and interventions.

The Public Goods Dilemma in the Context of COVID-19

The COVID-19 situation can be similarly conceptualized as a public goods game, because a virus-free environment constitutes a public good whose upkeep depends on people's joint commitment toward safety behaviors (Paakkari and Okan, 2020). Yet, because no one can be excluded from the benefits of a virus-free environment, the risk (and incentive) that people would choose not to cooperate and enjoy these benefits at the expense of others arises and culminates in the free-rider problem. Unwillingness to comply with public health guidelines has indeed emerged as a recurrent problem that severely undermines efforts to curtail the virus (Naso, 2020). For example, a substantial proportion of the American population refuses to wear masks (Kramer, 2020) despite evidence of their effectiveness in reducing infectiousness (Haischer et al., 2020). Community surveys also found that 39% of Americans do not intend to be vaccinated, with almost half of these individuals convinced that more information would not sway their decision (Funk and Tyson, 2020). These cases of noncompliance are not limited to the United States and they also include refusing to engage in social distancing (Murphy et al., 2020), resuming pre-pandemic social activities (Simonov et al., 2020), and failing to step up hygiene behaviors (Pan et al., 2020). As there is a level of social interaction that can be tolerated before the virus spreads exponentially in the population, people also have an incentive to engage in more social interaction than the carrying capacity allows, especially in the face of pandemic fatigue (Miller, 2020). The heterogenous effects of COVID-19 further contribute to differences in people's readiness to observe safety. Younger individuals who expect to have less serious symptoms from infection, for instance, have weaker incentives to act prudently (Coroiu et al., 2020). Anonymity in a large group coupled with other citizens following safety recommendations also reduces individual accountability and creates a safe zone for free riding to occur (Paakkari and Okan, 2020). Beyond individual-level noncompliance, the inability of some countries to manage COVID-19 domestically because of lax policies and inadequate responses has also contributed to global ineffectiveness in disease management when travel bans are lifted due to pressure to resume flights (Hymas, 2020). We are only as strong as our weakest links – "even if the share of such people is small, the collective consequences can be dire. In sum, even if some people follow social distancing measures for self-preservation reasons alone, the social average is likely to be substantially lower than the level required to eradicate the pandemic" (Cato et al., 2020, p. 51).

Recommendations to Reduce Free Riding and Increase Cooperation

EGT offers important insights on how the COVID-19 situation as a public goods dilemma could be tackled. Free riding has been shown to elicit negative emotions and perceptions of unfairness among cooperators, and humans seem naturally inclined toward identifying, punishing, and suppressing free-riding behaviors through social norms, sanctions, and imposing reputational costs, thus altering decision payoffs in favor of cooperation in public goods situations (Fehr and Gächter, 2000; Ostrom, 2000; Bowles and Gintis, 2011). For instance, vaccinated individuals showed less generosity toward their non-vaccinated counterparts who were perceived as violating the social contract, regardless of whether they came from the same or different social groups (Korn et al., 2020). As public goods confer significant fitness advantages, humans evolved a psychology that seeks to increase both the costs of free riding and the benefits of cooperation so that public goods can be sustained (Tooby et al., 2006; Cosmides et al., 2010). Knowledge of this evolved psychology can be useful in guiding the development of measures to protect a crucial public good like a virus-free and safe environment.

Using a game-theoretic approach to analyze COVID-19 behaviors, Cato et al. (2020) conceptualized safety benefits from social distancing (e.g., not dining out) as a public good and identified several social and psychological mechanisms that may inhibit free riding and increase people's likelihood

[2]Another way by which COVID-19 differs from previous pandemics is that while developed countries have historically had lower viral prevalence during pandemics, this is not the case for COVID-19 as global human development indices have been shown to be positively correlated with COVID-19 deaths (N = 168, r = 0.51; Luoto and Varella, 2021).

[3]Once more, this section serves to demonstrate how EGT has previously been used to analyze pandemic situations in general. Given the elusiveness of herd immunity for COVID-19, it is important to recognize limits to the applicability of the vaccination game for COVID-19.

of maintaining social distance. Based on a survey of 2,177 Japanese participants, the authors found that those who agreed that "it is important to always avoid doing anything people would say is wrong" were more apt to limit unnecessary social activity, thus indicating that public shame can promote safe behavior particularly when relational harmony and social obligations are regarded as important. Participants who indicated that they valued helping others and making others happy were also likelier to observe safety regulations, suggesting that altruistic and prosocial orientations promote cooperativeness (cf. Böhm et al., 2016).

As not everyone is altruistic or norm-abiding, voluntary-based policies can lead to insufficient compliance (Korn et al., 2020), thus necessitating the use of sanctions and punishments (e.g., legal enforcement and penalties for violations) to impose costs on noncompliance (Cato et al., 2020). State-enforced punishments are also important when social norms disincentivize people from calling out free riders at a communal level, such as when individuals face retaliation when they urge others to observe safety (Raihani and Bshary, 2015; Porterfield, 2020). Indeed, pool punishment (e.g., third-party punishers such as the police) is often preferable over peer punishment (e.g., laypersons who sanction others' misbehavior) as it facilitates the maintenance of order without disrupting the social fabric (Traulsen et al., 2012). That said, people tend to feel especially enraged when high-profile individuals such as politicians and celebrities get caught flouting rules and regulations (Bentham, 2020; Kok, 2020). As such individuals may exploit their influential status to escape punishment, anger can be adaptive in motivating laypersons to ensure that higher-status individuals remain accountable.

There are notable limits to the effectiveness of these mechanisms, in particular, the extrinsically motivated measures of shaming and punishment (Bénabou and Tirole, 2006; Jacquet et al., 2011). For example, worse outcomes may occur if shaming by ordinary citizens leads to stigmatization of infected persons, which can inadvertently make people hide their illness and hinder timely detection of the virus. In addition, the motivation to shame others can exacerbate intergroup tensions, such as when citizens utilize the COVID-19 situation to justify marginalizing outgroups (Habersaat et al., 2020; Prichard and Christman, 2020). Government-led punishment and enforcement can also be very costly. Punishment has proven to be a controversial strategy in the political context of a pandemic (Naso, 2020), especially when psychological reactance is triggered in individuals who misperceive the risks or have other priorities (May, 2005; Habersaat et al., 2020; we explore this issue further in the Discussion section). Moreover, the mobilization of police forces for surveillance and enforcement is a heavy expense when resources are needed across many other essential domains, and enforced lockdowns have also resulted in severe economic losses as the epicenters of infection are primarily metropolitan and commercial areas (Coibion et al., 2020). Considering these limitations, Cato et al. (2020) recommended the use of (1) voluntary- or nudge-based approaches as they carry low economic costs while preserving civil liberties and (2) moderate legal sanctions to address more serious cases of noncompliant behavior, but with some caveats: preferably when altruistic or other-regarding concerns are a feature of prevailing norms. As simple penalties such as fines can result in individuals feeling morally licensed to commit violations insofar as they pay the fee (Gneezy and Rustichini, 2000; Bowles and Polanía-Reyes, 2012), it is important that citizens care enough about how they are judged for reneging on social obligations for such punishments to have a desired effect.

Other Game-Theoretic Considerations

Inefficacies in COVID-19 management can be additionally explored with game-theoretic scenarios beyond the public goods game. In particular, some researchers have focused on the hesitancy of governments in enacting difficult but necessary virus containment measures (e.g., stay-at-home orders and lockdowns), as well as noncooperation for reasons other than free riding. For instance, Kabir and Tanimoto (2020) argued that because strict stay-at-home measures can greatly impact people's livelihoods, the cost of staying home (coupled with lockdown fatigue) can end up outweighing the risk of infection from going out. As individual-level decisions have a direct impact on the society-level effectiveness of stay-at-home orders, governments may refrain from implementing them because of anticipated low rates of compliance, especially from socioeconomically disadvantaged individuals who do not have the luxury of staying home (Blundell et al., 2020). Some governments may have also been hopeful that herd immunity from recoveries and vaccinations would allow them to avoid imposing such unpopular measures altogether (Weitz et al., 2020).

With rising numbers of cases and stretched health facilities, as well as the lack of a vaccine throughout 2020 and difficulties associated with achieving herd immunity for COVID-19 (Iwasaki, 2021; Sridhar and Gurdasani, 2021), government inaction became increasingly unviable. Hence, to increase people's adherence to strict regulations, Kabir and Tanimoto suggested using social programs such as emergency-relief funds and unemployment insurance to lower the costs of compliance, particularly for lower-paid workers (cf. Wilson, 2020; Wong and Wong, 2021). As vaccines became available at the end of 2020, Piraveenan et al. (2020) argued that programs driving vaccination uptake will surpass other aspects like vaccine efficacy and isolation procedures in importance. Using EGT, social network analysis, and agent-based modeling, the authors proposed that individuals' vaccination decision-making will be influenced by "demographics, physical location, the level of interaction, the health of the vaccine, epidemic parameters, and perceptions about the vaccine being introduced. Similarly, the decision-making of the government will be influenced by epidemic parameters, the nature of the vaccine being introduced, logistics, the management of human resources needed for the vaccination effort, and the amount of vaccine doses available" (Piraveenan et al., 2020, p. 11). In sum, holistic COVID-19 management would involve an appreciation of the many factors that calibrate payoffs so that both individual and governmental decisions shift toward safety.

DISCUSSION

A burgeoning literature has emerged in the wake of COVID-19 in recognition of the various lessons that can be gleaned from this experience, including studies of countries that have been relatively successful in managing the virus (e.g., Cousins, 2020; Wilson, 2020; Haslam et al., 2021). We suggest that more studies that view health safety as a public goods dilemma will prove highly illuminating and significantly contribute to disease management efforts. From this perspective, refusal to adhere to safety regulations reflects a free-riding strategy as noncooperative individuals capitalize on others' willingness to incur the costs of practicing safe behaviors without bearing those costs themselves. Our review highlights a comprehensive set of recommendations derived from EGT. Apart from containment measures, such as mask wearing, social distancing, and quarantine requirements and, eventually when vaccines are available, targeted programs to drive vaccination uptake, societal conditions that can reduce free riding and increase compliance are also crucial. From the top down, the enforcement of penalties that are commensurate with the degree of violation with an eye on potential side effects is needed. From the bottom up, social norms that foster altruistic attitudes as well as concern for relational harmony and the fulfillment of social obligations should be cultivated as they can promote cooperation in a less heavy-handed manner while also enhancing the effectiveness of top-down measures. Finally, the payoffs of compliance can be increased through subsidies for the disadvantaged alongside various other economic incentives. These measures are compatible with our evolved psychology for cooperation and holding noncooperators accountable, especially when people feel vested in the protection of cherished public goods.

Some debates exist over the importance of punishment in free-rider prevention. The backlash against sanctions in some countries notwithstanding, some researchers have also suggested that cooperation can occur without the need for punishment, particularly when group returns from individual contributions are non-linear (e.g., Kameda et al., 2011; Yong et al., 2021). The COVID-19 situation, however, demonstrates some necessity for heavy sanctions, particularly when social norms promoting voluntary cooperation are lacking. Noncompliance appears more severe in countries with highly individualistic orientations and low obedience to authority – where outright defiance against mask wearing and other health safety directives is not uncommon – compared to countries with high levels of collectivistic orientation and authority deference (Tan and Li, 2020; Gelfand et al., 2021). As it is easier to mobilize collective effort when people care about the public good and are willing to work together under the instruction of the authorities, norms that promote concern for relational harmony and social obligations coupled with willingness to abide by government regulations may be most effective in eliciting compliance. That said, noncompliance also occurs in authoritarian, collectivistic countries, albeit more furtively through secret activities such as illegal gatherings (Lim, 2020). Such transgressions continue to underscore the importance of sanctions and punishment, as voluntary goodwill may be insufficient to sustain the cooperation that is crucial for safety and yet highly fragile at a collective level (Bowles and Gintis, 2011; Naso, 2020).

The Emerging Role of Conspiratorial Thinking in Noncooperative Behavior

The growing problem of conspiracy theory-driven noncooperation is worth noting in the present context (Arnot et al., 2020; Prichard and Christman, 2020). As an epiphenomenon of adaptive rationalization mechanisms, conspiratorial thinking may be triggered as people struggle to gain a sense of control during crises such as COVID-19 (Yong et al., 2020). Distrust in societal institutions can further drive conspiratorial thinking and galvanize resistance against perceived threats (van Prooijen and van Vugt, 2018). Conspiracy theorists may, for instance, genuinely believe that COVID-19 is a hoax perpetuated by the "deep state," leading them to view their noncompliance as heroic, those who comply as weak or ignorant, and their accusers as evil (Collins, 2020). As such noncooperators have a substantially distinct understanding of the public goods at stake, analyses of their actions from a social dilemma perspective may be inadequate or even inappropriate, rendering many of the aforementioned strategies to induce cooperation (e.g., social disapproval and punishments) ineffective. Indeed, punishments imposed on them may be interpreted as persecution for their beliefs, which can inadvertently strengthen their worldviews and drive the growth of fringe clusters (Arnot et al., 2020). Dealing with such noncooperators requires a consideration of the characteristics of social networks (Kuga and Tanimoto, 2018) as well as measures that are presently outside the scope of EGT, such as controlling the spread of misinformation (Yong et al., 2020), influencing normative behavior through group identification and peer intervention (Arnot et al., 2020), and reducing perceptions of environmental hostility and inequality (van Prooijen and van Vugt, 2018). As the difficulty of spurring cooperation from conspiracy theorists also shows, a limitation of the public goods perspective is that solutions based on free-rider suppression may be more applicable in some environments than in others. Thus, further research is needed to develop improved EGT models that can address the unprecedented challenges associated with modern developments in social dynamics, such as globalization and information technology (Li et al., 2020).

Further Directions and Conclusions

In sum, we highlight both the relevance and limits of EGT for infectious disease situations and suggest that more studies, in particular, cross-national empirical investigations and research that extends EGT to novel scenarios, can contribute important insights on cooperation during COVID-19 and beyond. Further discussions on the complexities of applying EGT to design effective interventions in the COVID-19 context are also warranted as these are complex, iterative games that are concurrently happening in different ways around the world. Other evolutionarily driven directions may also enlarge our

understanding of behaviors in pandemic events alongside EGT, including cooperation versus competition as a function of threat (van Prooijen and van Vugt, 2018), inclusive fitness (Arnot et al., 2020), and adaptive leadership styles (Luoto and Varella, 2021), as well as risky behavior as a function of dominance signaling (Ronay and von Hippel, 2010) or life history strategies (Corpuz et al., 2020). Some of the research in these areas has indeed refined what we know about behaviors during COVID-19. For instance, although younger individuals have generally been observed to be less cautious and less compliant than older individuals (Coroiu et al., 2020), research that carefully examined the effects of life history while controlling for age has shown that life history strategy, but not age, was associated with COVID-19 precautions and projected behaviors (Corpuz et al., 2020). Through an integration of these perspectives with EGT, we are more likely to achieve a holistic understanding of dynamic, interdependent behaviors during pandemics and encourage compliance with public health guidelines in ways that work with rather than go against our evolved human nature.

AUTHOR CONTRIBUTIONS

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HYPOTHESIS AND THEORY
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COVID-19 Pandemic on Fire: Evolved Propensities for Nocturnal Activities as a Liability Against Epidemiological Control

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Humans have been using fire for hundreds of millennia, creating an ancestral expansion toward the nocturnal niche. The new adaptive challenges faced at night were recurrent enough to amplify existing psychological variation in our species. Night-time is dangerous and mysterious, so it selects for individuals with higher tendencies for paranoia, risk-taking, and sociability (because of security in numbers). During night-time, individuals are generally tired and show decreased self-control and increased impulsive behaviors. The lower visibility during night-time favors the partial concealment of identity and opens more opportunities for disinhibition of self-interested behaviors. Indeed, individuals with an evening-oriented chronotype are more paranoid, risk-taking, extraverted, impulsive, promiscuous, and have higher antisocial personality traits. However, under some circumstances, such as respiratory pandemics, the psychobehavioral traits favored by the nocturnal niche might be counter-productive, increasing contagion rates of a disease that can evade the behavioral immune system because its disease cues are often nonexistent or mild. The *eveningness epidemiological liability hypothesis* presented here suggests that during the COVID-19 pandemic, the evening-oriented psychobehavioral profile can have collectively harmful consequences: there is a clash of core tendencies between the nocturnal chronotype and the recent viral transmission-mitigating safety guidelines and rules. The pandemic safety protocols disrupt much normal social activity, particularly at night when making new social contacts is desired. The SARS-CoV-2 virus is contagious even in presymptomatic and asymptomatic individuals, which enables it to mostly evade our evolved contagious disease avoidance mechanisms. A growing body of research has indirectly shown that individual traits interfering with social distancing and anti-contagion measures are related to those of the nocturnal chronotype. Indeed, some of the social contexts that have been identified as superspreading events occur at night, such as in restaurants, bars, and nightclubs. Furthermore, nocturnal environmental conditions favor the survival of the SARS-CoV-2 virus much longer than daytime conditions. We compare the eveningness

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epidemiological liability hypothesis with other factors related to non-compliance with pandemic safety protocols, namely sex, age, and life history. Although there is not yet a direct link between the nocturnal chronotype and non-compliance with pandemic safety protocols, security measures and future empirical research should take this crucial evolutionary mismatch and adaptive metaproblem into account, and focus on how to avoid nocturnal individuals becoming superspreaders, offering secure alternatives for nocturnal social activities.

Keywords: pandemic (COVID-19), health measures, non-compliance behavior, chronotype (morningness–eveningness), evolutionary mismatch hypothesis, evolutionary psychology, life history theory, non-adherence

INTRODUCTION

Everything in pandemics is stamp collection except in the light of evolution. Evolutionary approaches to human behavior have the potential of uncovering hidden patterns and deep roots of many seemingly disparate findings (DeBruine, 2009; Gentle and Goetz, 2010; Stephen et al., 2014; Buss, 2020). And the context of pandemics, particularly the current COVID-19 context, is no different (Arnot et al., 2020; Dezecache et al., 2020; Seitz et al., 2020; Troisi, 2020; Luoto and Varella, 2021). Besides the evolved tendencies to respond to cues of diseases avoiding contagion (i.e., behavioral immune system; Shook et al., 2020; Stevenson et al., 2021), and to deal with pathogens (i.e., immune system; Krams et al., 2020), there are many other evolutionary factors that play a role in a pandemic situation (Arnot et al., 2020; Seitz et al., 2020). For instance, the evolved sex differences in psychological tendencies might help to explain why women are more careful and comply with safety measures more than men, and importantly why female leaders are more successful in minimizing deaths in a pandemic context than male leaders (Luoto and Varella, 2021). Further insight can be acquired via the evolutionary mismatch hypothesis (Lloyd et al., 2011; Li et al., 2018), in which evolved tendencies in response to specific ancestral contexts become a burden in current environments. Besides explaining the contemporary proliferation of mental health problems (Rantala et al., 2018, 2019, 2021), the evolutionary mismatch framework (Li et al., 2018) can also offer a heuristic and promising perspective into some maladaptive behaviors in the COVID-19 pandemics (Seitz et al., 2020).

This hypothesis and theory article aims to explore one instance of how evolutionary mismatch could help to explain disparate findings related to the current COVID-19 pandemic by uncovering a crucial factor possibly affecting the spread of the virus: the nocturnal psychobehavioral core of non-compliance to safety measures. In doing so, we suggest to take into account nocturnal risk-taking individuals in public health communications to improve compliance with virus-mitigating measures in order to possibly decrease the rate of contagion and superspreading events. However, application of behavioral science as public policy always needs to be made with extreme care and caution (IJzerman et al., 2020). We hope to both promote new discoveries and improve public policies, but also inspire scientists and policy-makers to use the advantages of an evolutionary perspective to help attenuate the consequences of the COVID-19 pandemic.

The main new hypothesis put forward here is *the eveningness epidemiological liability hypothesis*, which posits that evolved propensities for nocturnal activities, though adaptive in their own evolved context, have currently become a dangerous liability against epidemiological control. Although there were frequent and recurrent disease outbreaks in *Homo sapiens*' ancestral environment(s), the current SARS-CoV-2 virus seems to evade the evolved contagious disease avoidance tendencies because it makes individuals contagious before being symptomatic (e.g., Tindale et al., 2020) and it results in very mild or no symptoms in most individuals (Grant et al., 2020; Huff and Singh, 2020). This mismatch could be somewhat mitigated in Asian people, as it has been hypothesized that high levels of visceral adiposity in Southeast Asians might be an evolutionary response against previous encounters with coronaviruses in this region, but that Western populations lack this evolutionary adaptation against coronaviruses and could therefore be biologically more vulnerable to SARS-CoV-2 (Krams et al., 2020, 2021). Furthermore, there were probably few socially recommended restrictive virus-mitigating protocols and pro-health measures ancestrally, at least to the same extent that is now possible with the global proliferation of scientific information used to mitigate the COVID-19 pandemic.

The Relevance of Chronotypes to the COVID-19 Pandemic

Despite these evolutionarily novel societal protocols, evening-oriented individuals and others with a similar risk-taking psychobehavioral profile (e.g., Corpuz et al., 2020; Luoto and Varella, 2021) still tend to behave according to their evolved predispositions, creating an evolutionary mismatch (cf. Li et al., 2018; Ackerman et al., 2020; Dezecache et al., 2020; Seitz et al., 2020). Nocturnal individuals (i.e., those with a chronotype higher on eveningness, night-owls; Byrnes et al., 1999) tend to be more risk-taking, extraverted, impulsive, promiscuous, and have more pronounced Dark Triad personality profiles (i.e., psychopathy, Machiavellianism, narcissism) (cf. Digdon and Howell, 2008; Russo et al., 2012; Jonason et al., 2013; Fabbian et al., 2016; Sheaves et al., 2016; Díaz-Morales et al., 2019). Although evening-oriented individuals are also more intelligent (e.g., Randler, 2017), more capable of perceiving and understanding emotion (Stolarski and Jankowski, 2015), open to experience (Randler et al., 2017), and visually creative (Giampietro and Cavallera, 2007) than morning-oriented individuals, a great portion of their

profile aligns with the profile(s) so far found in individuals known to be likely to break COVID-19 pro-health rules. There is still a lack of direct and systematic evidence linking chronotype and compliance with pandemic safety measures, and the high similarity of both profiles deserves more attention from behavioral scientists and psychologists. We hope that by proposing our hypothesis, we inspire new research and stimulate the design of a more effective and persuasive communication of anti-contagion public policies.

The crucial task of reducing contagion and viral transmission is as much a problem of psychology and behavioral science as it is of epidemiology and virology (Kantor, 2020; Smith and Gibson, 2020; Van Bavel et al., 2020). Psychological factors play an essential role for the success of risk communication, endorsement of vaccines and antiviral therapies, compliance with hygiene practices and social distancing (Taylor, 2019). Many fields of psychology and social sciences have been mobilized to help create and promote health safety measures in order to slow the contagion rate of SARS-CoV-2 (Smith and Gibson, 2020; Van Bavel et al., 2020). About a third of individuals are non-adherent to preventive measures (e.g., Nzaji et al., 2020). Because there are some individuals and contexts that are more likely to generate superspreading events, and the available evidence shows that a ∼10% minority of superspreaders account for a large majority of the infections (Chang et al., 2020), even a small proportion of non-compliers can be very influential in worsening the transmission rate and throwing more gasoline into the pandemic fire (Wong and Collins, 2020).

First, we review the evolution of the use of fire that promoted the expansion of the nocturnal niche in humans (see section "The use of fire expanded the night-time activities"). The antiquity and recurrent fire control together with the difference between non-human ape and human sleep patterns indicates that over hundreds of millennia, humans have become gradually more nocturnal. Then, in order to refine the evolutionary consequences of that nocturnal expansion, we identify the key adaptive challenges that ancestral humans recurrently faced during night-time (i.e., its inherent imminent danger, peak tiredness, and easy concealment of identity) (see section "Night-time adaptive challenges"). Each of these challenges may have selected for an increased psychological tendency that together compose a part of the eveningness chronotype (i.e., the night-owl profile). Sexual selection and fast life history strategy probably play an important role in composing the eveningness chronotype (see section "Sexual selection for eveningness and fast life history strategies").

Further, we dissect the layers of related evolutionary mismatches and conflicting adaptive problems and show how there is a clash of core tendencies between the evening-oriented profile and the COVID-19 health safety protocols (see section "Evolutionary mismatches during the COVID-19 pandemic"). Then, we show that the available evidence on the individual-level predictors of non-compliance with the pandemic safety measures is very similar to that of the eveningness chronotype. We also show that some of the social contexts that have been identified as superspreading events occur during the night. Moreover, the new coronavirus is able to survive much longer in aerosols at night (see section "Eveningness epidemiological liability hypothesis").

We discuss the implications of the eveningness epidemiological liability hypothesis for explaining non-compliance with the pandemic safety measures via the ability of this multilevel evolutionary approach to organize disparate findings and open new lines of inquiry. Sexual selection and life history theory are the broader evolutionary dynamics within which we contextualize this model. We close with tentative suggestions for public health campaigns to target evening-oriented individuals, and for public authorities and private initiatives to promote, after careful consideration, epidemiologically secure alternatives for at least a part of their nocturnal social activities.

THE USE OF FIRE EXPANDED THE NIGHT-TIME ACTIVITIES

Vervet monkeys show less frequent predator-related behaviors (e.g., alarm calls) in recently burned habitats, suggesting that predators are less common in these areas, which in turn might explain survival advantages for human ancestors to initially pay attention to and follow the natural fires for defense purposes (Herzog et al., 2020). Humans have such an old and diversified contact with fire that they are considered the pyrophilic primate (Parker et al., 2016). The proposition that early hominins in Africa sporadically and opportunistically used fire around 1.6 mya (Roebroeks and Villa, 2011; Gowlett, 2016) matches the consequent onset of digestive adaptations for cooked food, e.g., gracile jaw and teeth (Wrangham, 2017), and the evidence for increased out-of-Africa migration toward colder locations (Gowlett, 2006; Brown et al., 2009). After the initial opportunistic phase, in which ancestral hominins were adapting to progressively dry, hence fire-prone environments (Parker et al., 2016), came a transitory phase that led to the habitual use of fire (Gowlett, 2016). Habitual use of fire dates to around 400–300 kya in Neanderthals and somewhat later in modern humans (Roebroeks and Villa, 2011).

Fire brought many benefits to our ancestors, such as heat and light, protection against predators and other nocturnal threats, sterilization, preservation, flavorization, easily digestible cooked food, and even aid in the manufacturing of tools (Wrangham, 2009; Dunbar and Gowlett, 2014). These advantages of fire control set the stage for socioecological (Dunbar and Gowlett, 2014), cognitive (Twomey, 2013), and cultural (Wiessner, 2014; Mithen, 2019) evolutionary change.

Among many other changes, the control of fire represents an important evolutionary factor toward increasing human nocturnal behaviors. Occasional nocturnal behavior is found in other apes such as in chimpanzees (Merker et al., 2015; Tagg et al., 2018) and in orangutans (Samson et al., 2014). Still, evidence indicates that modern humans did not merely retain the basic ape-like occasional nocturnal behaviors, but significantly expanded their nocturnal lifestyle. Modern humans in fact exhibit a derived sleep pattern that is different from the other apes. Human sleep is shorter, deeper, and exhibits more events of REM sleep which might have better maintained high levels of cognitive performance and freed nocturnal time for awake

activities (Samson and Nunn, 2015; Nunn et al., 2016). Indeed, in humans a considerable proportion of the population presents a stable and moderately heritable predisposition for night-time activity (e.g., Vink et al., 2001; Hur, 2007).

The use and control of fire in humans is ancient and recurrent (Roebroeks and Villa, 2011; Gowlett, 2016) enough to have acted as a strong selective pressure (Twomey, 2013; Dunbar and Gowlett, 2014; Wrangham, 2017). Aligned with the difference between ape and human sleep patterns (Samson and Nunn, 2015; Tagg et al., 2018), fire use provides compelling evidence indicating that humans indeed have expanded their nocturnal niche over hundreds of millennia (cf. Piffer, 2010; Putilov, 2014). Together with fire, many other selective pressures, such as increased predation risk in terrestrial environments, threats from intergroup conflict, and benefits arising from increased social interaction may have converged to expand evening-orientation in humans (Ponzi et al., 2015b; Samson and Nunn, 2015). Increased night-time activity may have amplified existing psychological variation in our species in response to key night-time adaptive challenges (cf. Marvel-Coen et al., 2018).

NIGHT-TIME ADAPTIVE CHALLENGES

The expansion into the nocturnal niche enabled by the use of fire posed new specific and recurrent adaptive challenges to ancient hominins, related to its inherent dangerousness, peak tiredness, and easy concealment of identity. Independently or in combination, these key features were probably relevant selective pressures that the ancestral populations faced in order to survive and benefit from the nocturnal niche. Particularly, the existing specific psychological variation that might have been adaptively reoriented and reorganized to deal with the key night-time challenges would have been effectively related to the correspondent variation in human chronotype.

Chronotype reflects individual underlying circadian rhythm (Jones et al., 2019). It is a psychophysiological concept that captures the natural individual variation in circadian well-functioning/preferences between 'morning types' all the way to 'evening types' on a continuous spectrum of sleep timing (Byrnes et al., 1999; Vink et al., 2001; Hur, 2007; Jones et al., 2019). There are morning lark individuals (i.e., with a chronotype higher on morningness, early to go to bed and early to wake up), intermediate individuals, and night-owl individuals (i.e., with a chronotype higher on eveningness, late to bed, late to wake up) (Byrnes et al., 1999; Vink et al., 2001; Hur, 2007; Jones et al., 2019).

Dangerousness

Night-time is universally dangerous and mysterious, because the diminished light makes it hard to foresee danger; what is more, there are typically fewer people around to alert and protect those who stay up late, thus increasing vulnerability. Darkness increases uncertainty, tension, and anxiety, which facilitates the acoustic startle reflex (Grillon et al., 1997), and leads to realistic/imagined fears of the dark (i.e., Nyctophobia) (Levos and Zacchilli, 2015), so much so that staring at a stationary point of light in the dark activates motion perception, generating an autokinetic illusion (i.e., the illusory movement of the light; Riedel et al., 2005), which is typical of agents.

There is an evolved and strategic shift in thresholds for signal detection when we feel in danger. Natural selection tends to select the less costly error particularly when the cost of not seeing a real threat (i.e., false negative) is greater than seeing an illusion of threat (i.e., false positive) (Haselton and Buss, 2000; Haselton and Nettle, 2006). Indeed, once in fear, the individual needs less evidence to trigger the threat reaction; thus, a higher rate of false alarms will be perceived, protecting against the cost of not perceiving a real threat (Tooby and Cosmides, 2008).

Because of the extended nocturnal niche, we might have developed a powerful and paranoid imagination, an evolved tendency to overestimate threats, purposes, and agency, particularly those stemming from enemies (Varella, 2018). In fact, Sheaves et al. (2016) showed that the eveningness chronotype is directly related to psychiatric symptoms of paranoia, hallucinations, anxiety, and depression. Large-sample genome-wide association studies have found shared underlying genetic pathways between eveningness chronotype and schizophrenia (Jones et al., 2016; Lane et al., 2016), and that being a night person is causally associated with worse mental health (i.e., less subjective well-being and more major depression) (Jones et al., 2019). Paranoid ideation and schizotypy predict conspiracy beliefs independent of sex (Darwin et al., 2011). Paranoia and belief in conspiracy are indeed positively correlated (Imhoff and Lamberty, 2018). Importantly, the anxiety and uncertainty experienced during epidemics and pandemics also tend to boost conspiracy thinking (Smallman, 2015, 2018; Taylor, 2019; Desta and Mulugeta, 2020).

At night, chances are higher to suffer from predator attacks (e.g., lions) in small-scale societies (Packer et al., 2011), or personal contact crimes in industrial societies (Averdijk and Bernasco, 2015). A similar level of dangerousness, if not worse, was possibly recurrent at night during ancestral times, given that the level of mortality in intergroup conflicts was substantial (Bowles, 2009), and ancestral hominids were preyed on by several large diurnal and nocturnal felines (Lee-Thorp et al., 2000; Treves and Palmqvist, 2007). This adaptive challenge could have selected for evening-oriented individuals to be more risk-taking and sensation-seeking, for them to be willing to face the elevated nocturnal risks. By facing the nocturnal risks, they could have served as guards for their significant others asleep (i.e., kin selection; Gardner et al., 2011), or they could have displayed to potential mates their survival qualities despite the handicap of vulnerability in the darkness (i.e., costly signaling in sexual selection; Grafen, 1990; Zahavi and Zahavi, 1999). Indeed, empirical studies indicate that chronotype variation leads to sleep asynchrony which function as protective night-time vigilance by having evening-oriented individuals as sentinels (Samson et al., 2017), and the sexual selection have also influenced the eveningness chronotype (Piffer, 2010; Randler et al., 2012b; Putilov, 2014; Ponzi et al., 2015a,b). Moreover, for protective

reasons, the *herd principle of 'security in numbers,'* which is for instance used as rows of nearby sleepers to insure night-time safety by Aboriginal settlements (Musharbash, 2013), as well as the equivalent *many eyes hypothesis* that is a predator-avoidance strategy which facilitates mixed-species bird flocking (Krams et al., 2020), could have been recurrently used in ancestral times, so much so that it would have selected for evening-oriented individuals to be gregarious, prioritizing social agglomerations. Human social conversational sounds could have indeed frightened ancestral predators, since large carnivores avoid human voices (Suraci et al., 2019). The nocturnal agglomeration and profusion of vocal sounds would have complemented the predator deterrent effect of fire (Wrangham, 2009; Dunbar and Gowlett, 2014).

Indeed, independent of sex and personality, individuals scoring higher on eveningness chronotype report higher risk-taking (Ponzi et al., 2014), sensation-seeking, and impulsivity (Russo et al., 2012; Antúnez et al., 2014). Men are, on average, more prone to risk-taking than women (Byrnes et al., 1999; Archer, 2019), and men aged 40 years and below are more nocturnal than women (Piffer, 2010; Fischer et al., 2017). Evening-oriented individuals also tend to be extroverted and have high openness to experience (Lipnevich et al., 2017), thus exhibiting the sociability to guarantee the 'security in numbers' through human vocal sounds around the fireplace, as currently done at the firelight talk among the Bushmen (Wiessner, 2014).

Peak Tiredness

During night-time, after the working hours, individuals are at their peak tiredness. This disrupts self-regulation and predisposes to impulsive behaviors, succumbing to immediate pleasures, such as cravings for food (Sevincer et al., 2016), alcohol and club/party drug use (Millar et al., 2019), and sexual intercourse (Refinetti, 2005; Jocz et al., 2018). Indeed, evening-oriented individuals have lower self-control (Digdon and Howell, 2008), which mediates their higher present orientation and instant gratification (Milfont and Schwarzenthal, 2014), are more impulsive (Cross, 2010), are more hedonistically present-oriented (Nowack and Van Der Meer, 2013; Stolarski et al., 2013; Borisenkov et al., 2019), use more alcohol and club/party drugs (Millar et al., 2019), and tend to smoke more (Randler, 2008; Wittmann et al., 2010; Patterson et al., 2016) than other chronotypes. Males exhibit lower self-regulatory capacities (Tetering et al., 2020), consume more alcohol (Salvatore et al., 2017), and are more nocturnal than females (Piffer, 2010; Fischer et al., 2017). However, women prefer to have sex later in the day than men (Jocz et al., 2018).

Identity Concealment

The lower visibility at night compromises individual recognition, thus favoring the concealment of identity which disinhibits behaviors previously repressed due to social desirability (Zhong et al., 2010; Hirsh et al., 2011). This sense of privacy lowers the risk for social reputational damage because it enables individuals to better control of external social interferences and manage the flow of information they emit (Klopfer and Rubenstein, 1977). This adaptive challenge, among others, could have selected for evening-oriented individuals to be more willing to engage in activities that go against social desirability, such as promiscuity, aggression, rule-breaking behavior, self-interested remorseless, and interpersonal manipulation. In effect, evening-oriented individuals are more prone to casual sex, cross-culturally (Cross, 2010; Piffer, 2010; Ponzi et al., 2015b; Matchock, 2018; Díaz-Morales et al., 2019), have a faster life history strategy (Ponzi et al., 2015b; Marvel-Coen et al., 2018), have first intercourse at an earlier age (Kasaeian et al., 2019), have higher tendencies toward aggression (Schlarb et al., 2014), exhibit higher rule-breaking behavior (Merikanto et al., 2017), and have higher Dark Triad personality traits, that is, Machiavellianism (e.g., exploitative behaviors), narcissism (e.g., self-orientation), and subclinical psychopathy (e.g., lack of empathy and remorse) (Jonason et al., 2013). Men, the more nocturnal sex (Piffer, 2010; Fischer et al., 2017), also exhibit higher propensity to casual sex (Schmitt, 2005; Hughes et al., 2020), higher aggression (Archer, 2004, 2019; Cross, 2010), and higher Dark Triad personality traits (Furnham et al., 2013).

Biological sex (male/female) is relevant in this analytical context: because males are more nocturnal than females, any other sex-differentiated trait favoring males would also appear in evening-oriented individuals. This does not happen with extraversion, which is related to eveningness (Lipnevich et al., 2017), and is higher in females (Schmitt et al., 2008). Moreover, evidence indicates that the nocturnal profile is not simply derived from or due to sex *per se*. In some cases, the relationship between a given chronotype and another trait is independent of sex (e.g., Ponzi et al., 2014), and of sex and age (e.g., Milfont and Schwarzenthal, 2014). In other instances, chronotype is the factor that slightly mediates the effect of sex on a given trait, not the other way around (Rahafar et al., 2017; Gowen et al., 2019). The majority of studies either control for sex (e.g., Merikanto et al., 2017), or conduct analyses separately for each sex. Hence, all this indicates that beyond sex, chronotype *per se* is an important factor for tracking intrasexual variation in psychobehavioral predispositions.

In summary, chronotype is indeed related to solving most of these nocturnal adaptive challenges. These psychological solutions and responses to the expansion of the nocturnal niche (i.e., paranoia, risk-taking, sensation-seeking and impulsivity, extraversion, lower self-control, promiscuity, aggression, rule-breaking, and dark personality traits) correspond to the evolved nocturnal profile (cf. Fabbian et al., 2016), a constellation of propensities tuned to nocturnal activities which have been adaptively helping humans to cope and benefit from the night-time for millennia. As noted earlier, not all facets of the nocturnal profile are socially undesirable: when compared with morning-oriented individuals, evening-oriented individuals exhibit higher general and emotional intelligence (e.g., Stolarski and Jankowski, 2015; Randler, 2017), are more open to experience (Randler et al., 2017), and visually creative (Giampietro and Cavallera, 2007). The stronger nocturnal sexual selection might also explain why they have high expression of traits such as intelligence, openness, and creativity which are desired in mate choice (Stone et al., 2012).

SEXUAL SELECTION FOR EVENINGNESS AND FAST LIFE HISTORY STRATEGIES

As applied in psychological research (Del Giudice et al., 2016; Nettle and Frankenhuis, 2020), life history theory offers a meta-theory (Hertler et al., 2018) and a mid-level established framework to interpret mainly childhood experiences, trait covariation, and individual differences in allocation of evolutionarily relevant resources (Del Giudice et al., 2016; Krams et al., 2019; Nettle and Frankenhuis, 2020). Organisms have limited amounts of time, energy, and resources at their disposal, that need to be allocated among competing demands. This leads to well-documented tradeoffs between different life history domains, most notably investing in survival (i.e., growth, self-maintenance, and immunity) or reproduction (i.e., short-term mating and competition vs. long-term mating and parenting) (Krams et al., 2019; Luoto et al., 2019; Laskowski et al., 2020; Lauringson et al., 2020; Rubika et al., 2020).

In combination with viability selection pressures (i.e., survival), part of the evidence compiled above also supports the influence of sexual selection on the evening-oriented chronotype (cf. Piffer, 2010; Randler et al., 2012b; Putilov, 2014; Ponzi et al., 2015a,b). More generally, the findings presented reflect a well-established 'fast' or 'slow' pattern of individual-level life history variation (Del Giudice et al., 2016; Del Giudice, 2020; Nettle and Frankenhuis, 2020), namely, a tradeoff between investing in immediate rewards and short-term mating vs. in parenting, longevity and health (Sherman et al., 2013; Ponzi et al., 2015b; Marvel-Coen et al., 2018). This evolved nocturnal profile contains elements considered to represent adaptive implementations of a fast life-history strategy (Ponzi et al., 2015b; Marvel-Coen et al., 2018), which prioritizes risky sexual behaviors and short-term rewards over pandemic-mitigating measures and health behaviors (Sherman et al., 2013; Luoto et al., 2019; Arnot et al., 2020; Corpuz et al., 2020). Men with higher symptoms of paranoid ideation tend to express faster life history traits, including a tendency toward casual sex (Kahl et al., 2020). Women find male risk takers over risk avoiders more attractive for short-term mating, and the opposite for long-term relationships (Sylwester and Pawłowski, 2011). Individuals high on sensation seeking have more casual sex partners (Penke and Asendorpf, 2008; Luoto et al., 2019). Extroverted men obtain a higher mating success (Randler et al., 2012b). Individuals with higher aggression tendencies have more casual sex partners (Cross, 2010). Individuals with higher Dark Triad personality traits have more casual sex partners, higher mating effort, and lower parenting effort (Valentova et al., 2020).

Besides the connection between each aspect of the nocturnal profile with mating success, promiscuity, and fast life history, these traits are also directly related to the evening-orientation, as we have established in the previous section (Ponzi et al., 2015b; Marvel-Coen et al., 2018). Evening-oriented individuals cross-culturally exhibit higher tendencies for short-term mating and, indeed, have more casual sex (Cross, 2010; Piffer, 2010; Gunawardane et al., 2011; Ponzi et al., 2015b; Matchock, 2018; Díaz-Morales et al., 2019). Evening-type men are more flirtatious in the later part of the day (Gunawardane et al., 2011), have a higher propensity to stay out late (Randler et al., 2012b), and have higher intrasexual competition tendencies (Ponzi et al., 2015a). Evening-orientation is related to higher testosterone in men (Randler et al., 2012a), and testosterone also coordinates life history strategies across species (Luoto et al., 2019). Hence, the evening-oriented chronotype has been considered to be implementing a fast life history strategy (Ponzi et al., 2015b; Marvel-Coen et al., 2018).

All this nocturnal mating action likely results from creation of an evening lek for displaying various behaviors advertising desirable qualities through courtship (Piffer, 2010; Putilov, 2014). The primary mating ground of most modern humans (besides online dating) seems to be dancing bars and nightclubs, where people flirt and dance using their bodies to negotiate space (Nofre et al., 2017), and display sexually desirable qualities to find sexual partners (e.g., Röder et al., 2016). Correspondingly, there is a 50% increase of coupled individuals leaving the nightclub as compared to those entering it (Mannion et al., 2009). There is a distinction in mate search locations between the short-term and long-term niches, and the short-term niche includes many night-time activities, such as bars, nightclubs, parties, dance clubs, weddings, concerts, and fraternity parties (Jonason et al., 2015). The use of short-term mating locations is positively related with short-term mating orientation. And there is no sex difference in the conceptualization of which locations constitute appropriate short-term or long-term mating niches (Jonason et al., 2015).

Indeed, as a result of this temporal mating niche differentiation, individuals with a similar chronotype tend to mate assortatively (Randler and Kretz, 2011). This homogamy could be the evolutionary process promoting trait covariation (cf. Štěrbová and Valentova, 2012; Varella et al., 2012; Štěrbová et al., 2017; Conroy-Beam et al., 2019; Nishi et al., 2020) between the eveningness chronotype and the constellation of nocturnal psychobehavioral activities. For instance, behavioral genetic evidence has shown that 80% of the positive relationship between eveningness chronotype and externalizing behaviors (i.e., aggression and rule-breaking behavior) is accounted for by shared genetic influences between both tendencies, i.e., chronotype and antisocial tendencies (Barclay et al., 2011). The promiscuous short-term orientation in addition to assortative mating stressed here might better explain the high mating success of eveningness-oriented individuals than the degree of mate choosiness (cf. Staller and Randler, 2021).

The increased nocturnal sexual activity, including short-term mating-orientation and intrasexual competition, strengthened the pressure of sexual selection acting during nocturnal social contexts (cf. Piffer, 2010; Putilov, 2014). These factors converge and relate to the evidence that human sleep patterns present two hallmarks of a sexually selected trait. First, men exhibit shorter sleep and a more evening-oriented chronotype (Piffer, 2010; Randler, 2016; Fischer et al., 2017). Second, the ontogenetic phase immediately after puberty which is most typical of mating effort (i.e., late adolescence and young adulthood) is when individuals are most evening-oriented, and the sex difference fades during women's menopause (Piffer, 2010; Randler et al., 2012b; Fischer et al., 2017).

EVOLUTIONARY MISMATCHES DURING THE COVID-19 PANDEMIC

A careful analysis of the ancestral versus modern, the recurrent versus rare, and convergent versus conflicting facets of selection pressures offers a complex and detailed picture of the relationship between eveningness chronotype and non-compliance with virus-mitigating public health protocols. Evolutionary mismatches have a variety of configurations, causes, and outcomes (Li et al., 2018; Rantala et al., 2019, 2021). They can be caused by a natural or human-made change in the environment that disrupts the fit between evolved adaptation and its respective ancestral recurrent selective regime (Li et al., 2018). The environmental change can be forced or hijacked, impacting an adaptation's specific input, its existence, intensity, or by replacement of the original input by a similar one (Li et al., 2018). The consequences of mismatches can be undesirable or desirable for the individual, and they can have decreasing or increasing effects on fitness (Li et al., 2018). Furthermore, because we are dealing with two different domains (namely, chronotype, and disease avoidance) there is the possibility of convergent or conflicting selection pressures between the domains. Conflicting adaptive problems constitute an *adaptive metaproblem* (Al-Shawaf, 2016; Rantala et al., 2019). In contrast, the alignment of adaptive problems can be said to constitute an *adaptive problem-merging*. The incongruence and/or congruence between different adaptive problems can be ancestral or new, recurrent or rare. Thus, although they are independent processes, evolutionary mismatches and interaction between different adaptive problems relate to each other.

Mismatch #1: Absence of Disease Cues Enabling the New Coronavirus to Evade Our Evolved Pathogen Avoidance Defenses

Contagious disease outbreaks and epidemics were a recurrent aspect of human ancestral environments (Fumagalli et al., 2011; Deschamps et al., 2016), so much so that beyond our evolved immune system, a growing literature has emphasized the existence and special features of the behavioral immune system (BIS) as a constellation of proactive and reactive tendencies promoting contagion avoidance (Ackerman et al., 2018, 2020; Troisi, 2020). Direct and indirect cues of diseases are relevant inputs to trigger the touch avoidance and distancing reactions of the BIS (Miller and Maner, 2012; Ackerman et al., 2018). Other highly social species also have evolved contagion avoidance reaction toward conspecifics with contagious diseases (e.g., Loehle, 1995; Behringer et al., 2006). Hence, it would be expected that humans activated similar pathogen avoidance mechanisms during the current pandemic times (cf. Troisi, 2020; Stevenson et al., 2021). Many individuals are indeed triggered by the current epidemiological threat and are socially distancing to avoid contagion (Makhanova and Shepherd, 2020), particularly women (e.g., Galasso et al., 2020), who are, on average, more disgust-sensitive and anxious about contagion (Druschel and Sherman, 1999; Fleischman, 2014; Luoto and Varella, 2021) and reported higher level of anxiety during the current COVID-19 pandemic (Semenova et al., 2021).

However, the SARS-CoV-2 virus seems to evade some of the evolved contagion-avoidance adaptations of humans (Ackerman et al., 2020; Seitz et al., 2020; though see Krams et al., 2020, 2021), because infected individuals are contagious before manifesting any symptoms (Tindale et al., 2020), not all infected individuals will manifest any symptoms (i.e., they are asymptomatic) (Cheng et al., 2020; Huff and Singh, 2020), not all symptoms will be present in every infected symptomatic individual, not all symptoms will be easily detectable (e.g., fever, fatigue), the majority of infected symptomatic individuals will develop only a mild version of COVID-19 and will survive, and the incapacitation or death of those few individuals with severe COVID-19 cases will only occur a few weeks after contagion (Grant et al., 2020). All this creates a natural evolutionary mismatch in which the input of a disease necessary to trigger the pathogen avoidance response in others is attenuated or absent (Fraser et al., 2004; Ackerman et al., 2020; Seitz et al., 2020). Further, the hospitalization, cremation, and burials in urban settings do not occur in areas where most people could easily go and verify the numbers of severe cases and deceased first-hand. This adds a layer of human-made mismatch to this domain. Probably, this mostly natural but also human-made evolutionary mismatch of attenuated or absent input within the contagious disease avoidance domain (#1) is responsible for a portion of the current non-compliance with safety measures and transmission-mitigating rules (cf. Fraser et al., 2004; Gandhi et al., 2020). This is further complicated by the tendency in which people affiliate and seek social contact even more when exposed to a threat (Dezecache et al., 2020).

For the majority of individuals who do their utmost to avoid exposure to the virus during the current COVID-19 pandemic (Makhanova and Shepherd, 2020; Nzaji et al., 2020), it has been individually undesirable to stay socially isolated at home (cf. Dezecache et al., 2020; Hwang et al., 2020), advantageous for survival, but at the same time disadvantageous for short-term mate search because it decreased their nocturnal activities (e.g., bars, discos, and nightclubs) (cf. Mannion et al., 2009; Ponzi et al., 2015b; Díaz-Morales et al., 2019). These conflicting domains of adaptive problems comprise an adaptive metaproblem (Al-Shawaf, 2016; Rantala et al., 2019). It is possible that among other factors, such as sex, age, and life history strategy, the level of individual nocturnal tendencies and disease avoidance are moderating factors in determining whether or not an individual trades off mating for survival (or vice versa) during this pandemic (cf. Corpuz et al., 2020; Makhanova and Shepherd, 2020). On the other hand, without conspicuous symptoms and first-hand experiences of COVID-19 outcomes triggering disease avoidance mechanisms (Ackerman et al., 2020; Gandhi et al., 2020; Seitz et al., 2020), most individuals who are less anxious about contagion might simply try to continue their normal lives even in modern pandemic times. For them, there will be no conflicting adaptive problem because the disease-aversion domain would be less or not at all activated.

Mismatch #2: Artificial Lighting Extending the Evolved Eveningness in Contemporary Life

The evolved propensities of evening-oriented individuals would have long been ancestrally adapted and still currently adaptive under normal nocturnal circumstances (Piffer, 2010; Putilov, 2014). However, since the late industrial age after the human-made diffusion of artificial lighting there has been a further nocturnalization of Western life (Koslofsky, 2011; Vollmer et al., 2012; Rantala et al., 2021). This is further intensified by the screen devices that keep us eagerly focused after sunset and the new wave of blue led lights that strongly suppress the endogenous production of melatonin, the sleep hormone (West et al., 2011; Vollmer et al., 2012; Walker et al., 2020). Thus, it is a case of a human-made, hijacked, input substituted and intensified (because the sunlight that naturally inhibits melatonin is being substituted by artificial light and intensified in the case of blue led lights), individually desirable, and, possibly, fitness-enhancing evolutionary mismatch (#2) (though see Rantala et al., 2021, for the maladaptive outcomes associated with this mismatch).

Mismatch #3: Virus-Mitigating Social Restrictions Disrupting Evolved Social Life; Evening-Oriented Individuals More Likely to Resist in Favor of Their Ancestral Evolved Tendencies

During the current pandemic, there has been another new human-made environmental change that disrupted normal daily and nocturnal activities: the forced official epidemiologically informed protocol for mitigating viral transmission and for providing public health guidance: beware of the virus and the disease, avoid social gatherings, control your hand movements, maintain improved hygiene, cleanliness, and increase interpersonal space, shelter at home, ventilate indoor settings, avoid multiple intimate contacts with people beyond your close social circle, wear a face mask when outside in order to protect others, and care for the safety of vulnerable ones (cf. Centers for Disease Control and Prevention [CDC], 2020). Although humans have an evolved dispositional tendency to avoid touching or getting in close proximity with sick individuals and to socially distance and attend to hygiene in times of outbreaks (cf. Hewlett and Hewlett, 2007; Ackerman et al., 2018), the specificities of the SARS-CoV-2 virus do not fully trigger psychobehavioral pathogen avoidance mechanisms (the #1 mismatch) (Ackerman et al., 2020; Gandhi et al., 2020; Seitz et al., 2020). Moreover, in ancestral times there were probably no requirements for using face masks, or soap, nor high-concentration alcohol for disinfection during outbreaks, not even the knowledge of why those measures are crucial to mitigate viral transmission and decrease avoidable death rates. Thus, even though there is now almost a year of evolutionarily novel societal protocols used to curb the spread of the SARS-CoV-2 virus, evening-oriented individuals, those who are highly interested in making new social contacts during the night, and those with fast life history strategies may be inclined to continue behaving according to their evolved predispositions (Piffer, 2010; Putilov, 2014; Corpuz et al., 2020; Luoto and Varella, 2021), constituting an evolutionary mismatch (cf. Li et al., 2018; Ackerman et al., 2020). This is the current culturally enacted, human-made, individually undesirable, but fitness-enhancing evolutionary mismatch (#3) that quite possibly made evening-oriented individuals a dangerous liability against epidemiological control. This is because of the previously described mismatches (#1 and #2), and because the core message of the pandemic public health guidance virus-mitigating rules (i.e., focus on survival and refraining from social contact; Centers for Disease Control and Prevention [CDC], 2020; World Health Organization, 2020) clashes with the eveningness profile (cf. Fabbian et al., 2016), which is related to exhibiting paranoia (Sheaves et al., 2016) (paranoia is positively related to conspiracy beliefs, Darwin et al., 2011; Imhoff and Lamberty, 2018), risk-taking (Ponzi et al., 2014), sensation-seeking and impulsivity (Russo et al., 2012; Antúnez et al., 2014), extraversion (Lipnevich et al., 2017), unrestrained hedonism (e.g., Millar et al., 2019), low self-control (Digdon and Howell, 2008), present orientation (e.g., Borisenkov et al., 2019), alcohol, cigarettes, and substance use in public places together with others (Patterson et al., 2016; Millar et al., 2019), multiple short-term mating tendencies (e.g., Díaz-Morales et al., 2019), fast life history (e.g., Marvel-Coen et al., 2018), rule-breaking tendencies (Merikanto et al., 2017), and self-centered remorseless exploitation of others (Jonason et al., 2013), thus trading survival and health-concern for prioritizing sensation-seeking and mating opportunities. During the current pandemic, on average, the evening-oriented profile might put the population at risk by engaging in acts, exhibiting attitudes, and creating contexts that promote and sustain human-to-human contagion.

Mismatch #4: Pre-pandemic Culturally Imposed Morning-Orientation Leading to Social Jetlag in Evening-Oriented Individuals

Interestingly, the same virus-mitigating COVID-19-mandated social restrictions might have diminished the human-made culturally induced evolutionary mismatch of having schools, universities, and workplaces biased toward the morning rather than the evening part of the day (#4). This social time pressure mismatch has created a social jetlag in which evening-oriented individuals exhibit massive sleep deficit negatively influencing their bodily and mental health (Korman et al., 2020). However, the COVID-19-mandated social restrictions have relaxed the social time pressure related to social jetlag so individuals can sleep longer and later. A study on 25,000 Argentinians (Leone et al., 2020), another cross-national study on 3,787 participants (Rome et al., 2020), another study on 7,517 participants from 40 countries (Korman et al., 2020), and another cross-national study involving 11 countries on 14,000 participants (Roitblat et al., 2020) showed that COVID-19 related lockdowns and social restrictions have themselves induced significant delays in chronotype. The current weakening of mismatch #4 (morning social pressure) plus the increase of mismatch #2

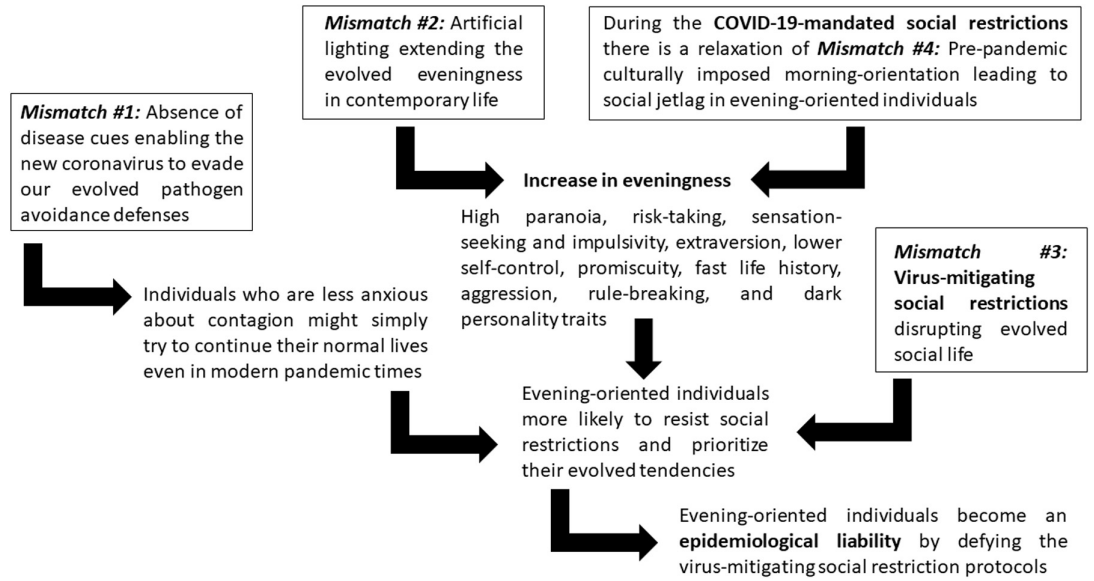

FIGURE 1 | The relationship among the four mismatches and their consequences in relation to the eveningness epidemiological liability hypothesis.

(artificial lighting) may have converged in increasing evening orientation, which might further complicate the epidemiological liability of mismatch #3 (nocturnal individuals defying the virus-mitigating social restriction protocols). **Figure 1** summarizes the connections between the four mismatches and their consequences as the conceptual foundation for the eveningness epidemiological liability hypothesis.

Four Mismatches Underlie the Eveningness Epidemiological Liability Hypothesis

This sequence of four mismatches culminating in the incongruence between evening-type and compliance with virus-mitigating safety protocols is of crucial relevance for promoting new ways of convincing night-owl individuals to comply with the best practices of pandemic control. The literature on the evolution of disease transmission modes, such as vertical (mother to offspring), or horizontal (sexual, non-sexual/direct contact, airborne, environmental/water/food, fomites/objects, and vector-borne) (Antonovics et al., 2017) should incorporate individual variation in chronotype. Arguably, pre- or asymptomatically contagious infectious diseases (cf. Fraser et al., 2004; Ackerman et al., 2020) which are disseminated by air, direct contact, or sexual activities might create a mismatch in which evening-oriented individuals would be a greater liability against epidemiological control protocols (mismatch #3). If this situation were recurrent enough in the ancestral environment, after higher infections rates and stronger natural selection acting on evening-oriented individuals, we would expect to find in evening-oriented individuals a high evolved resistance against those pathogens using the modes of transmissions that make evening-oriented individuals easier targets for being more promiscuous (e.g., Matchock, 2018; Díaz-Morales et al., 2019) and gregarious (Lipnevich et al., 2017) than morning-oriented individuals, for instance. In contrast, pre- or asymptomatically contagious infectious diseases transmitted by water or mosquitoes' bites would affect evening-oriented individuals less or equally as morning-oriented individuals. Thus, because not all ancestral disease outbreaks were spread through airborne transmission or through sexual intercourse (e.g., STDs), or had mostly asymptomatic cases, and because there was no precise means or know-how on virus-mitigating measures, evening-oriented individuals were not always a liability against epidemiological control ancestrally. Nevertheless, during the current pandemic, these factors converge leading to the eveningness epidemiological liability hypothesis.

EVENINGNESS EPIDEMIOLOGICAL LIABILITY HYPOTHESIS

In fact, a growing body of research has shown that individual traits interfering with social distancing and anti-contagion measures are typical of the nocturnal type. Research on personal factors related to non-compliance with the pandemic safety best practices are still in the initial phases, but it is already possible to see an emerging pattern. The COVID-19 health rule-breakers, i.e., those contributing to non-compliance with the epidemiological safety guidance during the new coronavirus pandemic, tend to be males (Coroiu et al., 2020; Galasso et al., 2020; Nivette et al., 2020; Pollak et al., 2020; Sobol et al., 2020; Tomczyk et al., 2020), exhibit higher proneness to paranoia (Kowalski et al., 2020), and conspiracy beliefs (Biddlestone et al., 2020; Kowalski et al., 2020; Romer and Jamieson, 2020), show higher risk-taking (Miguel et al., 2020; Pollak et al., 2020; Zirenko et al., 2020), tend to not fear the virus, have low perceived risk of COVID-19 (Harper et al., 2020; Pollak et al., 2020),

exhibit low self-control (Boylan et al., 2020; Nivette et al., 2020), use more alcohol and drugs (Taylor et al., 2020), tend to be smokers (Pollak et al., 2020), tend to be extraverted (Götz et al., 2020), tend to perceive more mating opportunities (e.g., potential sexual or romantic partners) (Zajenkowski et al., 2020), not have children (Pollak et al., 2020), have faster life history strategies (Corpuz et al., 2020), lower agreeableness (Asselmann et al., 2020; Zajenkowski et al., 2020), lower empathy (Miguel et al., 2020; Zirenko et al., 2020), higher levels of callousness and deceitfulness (Miguel et al., 2020), antisocial potential and moral disengagement from prevention rules (Nivette et al., 2020), higher psychological entitlement (i.e., high expectations for good outcomes, a lack of concern about others, and a distrust of authority figures) (Zitek and Schlund, 2020), and higher Dark Triad personality traits (i.e., Machiavellianism, psychopathy, and narcissism) (Nowak et al., 2020; Zajenkowski et al., 2020; Zirenko et al., 2020).

During the COVID-19 pandemic, non-compliant individuals also tend to be younger (i.e., adolescents and young adults) (Coroiu et al., 2020; Park et al., 2020; Tomczyk et al., 2020). There is ontogenetic variation in human chronotype: evidence indicates a shift toward later chronotype (i.e., higher eveningness) during adolescence, reaching a peak in eveningness at around 19 years, then shifting back toward earlier chronotype (i.e., morningness) thereafter (Randler, 2016; Fischer et al., 2017). Individuals non-adherent to the preventive measures of the pandemic tend to have high levels of ADHD and high psychological distress (Pollak et al., 2020). Evening-oriented individuals are more represented among those with mental disorders (e.g., anxiety, depression, psychosis, and bipolar) and are in general associated with higher psychological distress and symptom severity (Fares et al., 2015; Fabbian et al., 2016; Jones et al., 2016, 2019; Lane et al., 2016; cf. Rantala et al., 2021). **Table 1** displays a case-by-case comparison between each facet of the eveningness profile and the non-compliance profile.

Aligned with the similarities between the evening-oriented profile and the non-complier profile, some of the social contexts of high contagion risk (and situations that have been identified as superspreading events) occur at night. For instance, in Hong Kong the largest cluster of transmission network, the 'bar and band' cluster, was traced back to a series of bars totaling 106 infected individuals; for comparison, daytime transmission events, such as a wedding cluster and a temple cluster, had far fewer infections (22 and 19 infected people, respectively: Adam et al., 2020). In Chicago, full-service restaurants had the largest impact on infections, consecutively followed by fitness centers, cafes, and snack bars, hotels and motels, limited-service restaurants, and religious organizations (Chang et al., 2020). In Madison, a cluster with 20 bars had a visitation rate that was positively related to infection rates, and was

TABLE 1 | Comparison between the eveningness profile and the profile of those who are non-compliant with the virus-mitigating pro-health measures.

Eveningness profile	Non-compliant profile
High in males (Fischer et al., 2017; Piffer, 2010)	Often males (Coroiu et al., 2020; Galasso et al., 2020; Nivette et al., 2020; Pollak et al., 2020; Sobol et al., 2020; Tomczyk et al., 2020)
Peak in eveningness at around 19 years (Randler, 2016; Fischer et al., 2017)	Tend to be adolescents and young adults (Coroiu et al., 2020; Park et al., 2020; Tomczyk et al., 2020)
High symptoms of paranoia, hallucinations (Sheaves et al., 2016)	High proneness to paranoia (Kowalski et al., 2020), and conspiracy beliefs (Biddlestone et al., 2020; Kowalski et al., 2020; Romer and Jamieson, 2020)
High risk-taking (Ponzi et al., 2014), sensation-seeking, and impulsivity (Russo et al., 2012; Antúnez et al., 2014)	High risk-taking (Miguel et al., 2020; Pollak et al., 2020; Zirenko et al., 2020), do not fear the virus, have low perceived risk of COVID-19 (Harper et al., 2020; Pollak et al., 2020)
High extroversion and openness to experience (Lipnevich et al., 2017)	High extroversion (Götz et al., 2020)
Low self-control (Digdon and Howell, 2008; Milfont and Schwarzenthal, 2014), high impulsiveness (Cross, 2010), high present-orientation (Nowack and Van Der Meer, 2013; Stolarski et al., 2013; Borisenkov et al., 2019), high use of alcohol and club/party drugs (Millar et al., 2019), and tend to smoke often (Randler, 2008; Wittmann et al., 2010; Patterson et al., 2016)	Low self-control (Boylan et al., 2020; Nivette et al., 2020), high use of alcohol and drugs (Taylor et al., 2020), tend to be smokers (Pollak et al., 2020)
Fast life history strategy (Ponzi et al., 2015a,b; Marvel-Coen et al., 2018), high promiscuity (Cross, 2010; Piffer, 2010; Ponzi et al., 2015b; Matchock, 2018; Díaz-Morales et al., 2019), have first intercourse at an earlier age (Kasaeian et al., 2019)	Fast life history strategy and promiscuity (Corpuz et al., 2020), high perception of mating opportunities (e.g., potential sexual or romantic partners) (Zajenkowski et al., 2020)
High tendencies toward aggression (Schlarb et al., 2014), rule-breaking behavior (Merikanto et al., 2017), and Dark Triad personality traits, that is, Machiavellianism (e.g., exploitative behaviors), narcissism (e.g., self-orientation), and subclinical psychopathy (e.g., lack of empathy and remorse) (Jonason et al., 2013)	Low agreeableness (Asselmann et al., 2020; Zajenkowski et al., 2020), low empathy (Miguel et al., 2020; Zirenko et al., 2020), high levels of callousness and deceitfulness (Miguel et al., 2020), have antisocial potential and moral disengagement from prevention rules (Nivette et al., 2020), high psychological entitlement (i.e., high expectations for good outcomes, a lack of concern about others, and a distrust of authority figures) (Zitek and Schlund, 2020), high Dark Triad personality traits (i.e., Machiavellianism, psychopathy, and narcissism) (Nowak et al., 2020; Zajenkowski et al., 2020; Zirenko et al., 2020)
High prevalence of mental disorders (e.g., anxiety, depression, psychosis, and bipolar), and high psychological distress and symptom severity (Fares et al., 2015; Fabbian et al., 2016; Jones et al., 2016, 2019; Lane et al., 2016)	High levels of ADHD and high psychological distress (Pollak et al., 2020)

larger than that of a cluster of 68 restaurants (Harris, 2020). In Vietnam, among other superspreading events, Chau et al. (2020) reported a superspreading event in a bar. In South Korea, among other instances of superspreading situations, Kang et al. (2020) traced back 96 primarily infected individuals from the Seoul nightclubs, and consequently, another 150 secondary and subsequent infections. Among other possibilities, such as private social gatherings or workers living in close quarters, outbreaks in Florida, Texas, California, the Montréal metropolitan area, and in Spain (Catalunya and Aragón) were also linked to the reopening of indoor dining, bars, and nightclubs (Althouse et al., 2020). Although the nocturnal superspreading events are not the only instances of such events, this evidence from across the world strengthens the case for a common nocturnal core of non-compliance during this pandemic.

Moreover, because there is no sunlight and it is colder during night-time, the virus has better survival conditions: it can survive in aerosols more than 2 h at night or indoors, while surviving only 4.8 min at 40°C, 20% humidity, and high intensity sunlight equivalent to noon on a clear summer solstice day at 40°N latitude (Dabisch et al., 2020). This line of evidence connects both previous lines of evidence and strengthens the case for considering the importance of eveningness chronotype as a potential epidemiological liability during the COVID-19 pandemic.

In sum, the psychobehavioral profiles of those non-compliant with health measures are strikingly similar to those of evening-oriented individuals, with both profiles aligned with fast life history strategies and a neglect of health measures and precautions (Arnot et al., 2020; Corpuz et al., 2020). Some night-time activities such as dining in restaurants and attending bars and nightclubs have been linked to superspreading events; at night there is less health measure enforcement; and at night as well as indoors, the virus has environmental conditions enabling its persistence in aerosol for longer than outdoors during the day. **Figure 2** summarizes the three different sources of evidence so far supporting the eveningness epidemiological liability hypothesis. This confluence of factors suggests that epidemiologists, behavioral scientists, psychologists, and policy-makers seeking to minimize the spread of the virus should carefully consider the eveningness chronotype and night-time activities.

DISCUSSION

The eveningness epidemiological liability hypothesis presented here connects disparate strands of research guided by an evolutionary mismatch approach and life history theory (cf. Ackerman et al., 2020; Corpuz et al., 2020; Seitz et al., 2020), highlighting the possibility that there is a nocturnal psychological core underlying the disposition toward non-compliance to virus-mitigating safety measures during the COVID-19 pandemics. We have presented the evolutionary timeline and context in which, after the habitual use of fire, the consequent expansion of nocturnal activities has amplified some psychological traits in our species, which are related to solving the key adaptive problems occurring nocturnally: its inherent dangerousness, peak tiredness, and easy concealment of identity. Those adaptive challenges have selected for nocturnal individuals to be more paranoid, brave, impulsive, promiscuous, rule-breaking, and gregarious yet antisocial. This fast life-history profile (cf. Marvel-Coen et al., 2018; Arnot et al., 2020), which trades survival and health for prioritizing short-term mating opportunities directly

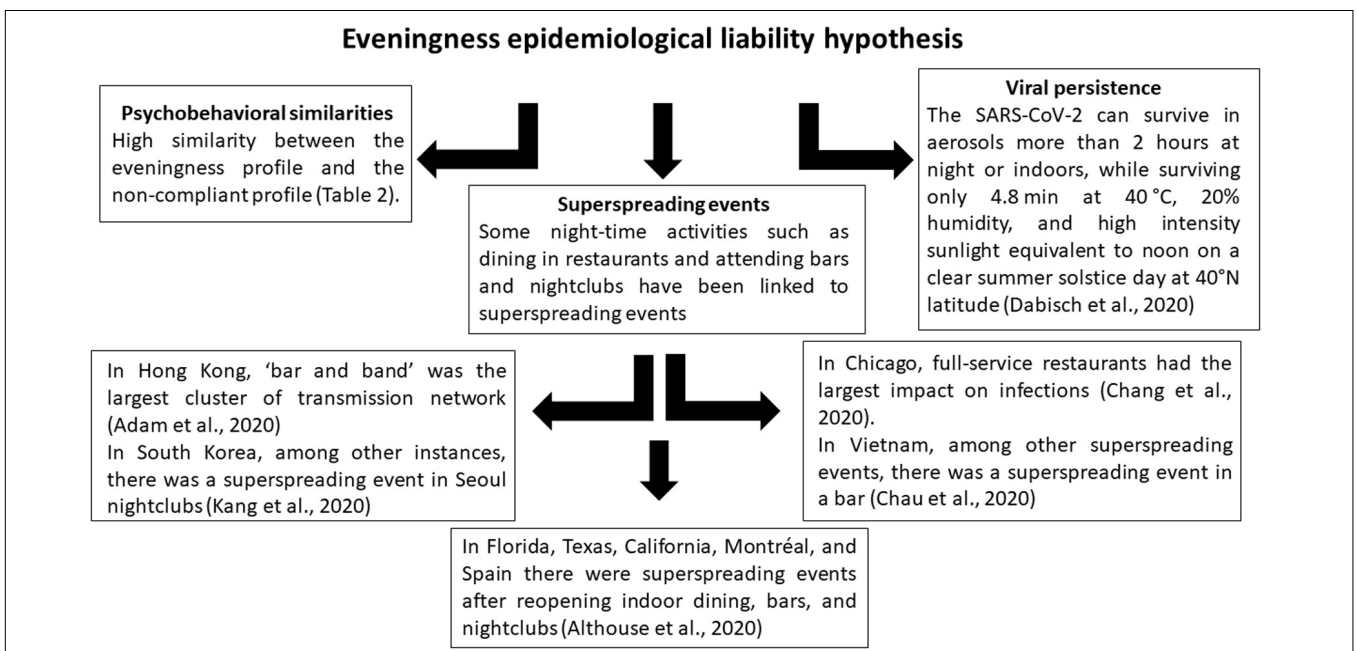

FIGURE 2 | Three sources of available evidence supporting the eveningness epidemiological liability hypothesis.

clashes with the core message of the pandemic public health protocols (e.g., Corpuz et al., 2020): focus on survival and refrain from social contact. In the current modern globalized and urbanized context, the increase of use of artificial light after dawn and the relaxation of social time pressure for early activity after pro-health mandatory protocols for social restriction both have contributed to nocturnalization of individuals (West et al., 2011; Vollmer et al., 2012; Korman et al., 2020; Leone et al., 2020; Rome et al., 2020), which may have further complicated the epidemiological liability of evening-oriented individuals as non-compliers. Although cross-culturally population density is not related to COVID-19 infection rates (Krams et al., 2021), the potential anonymity provided by large metropolitan cities that 'never sleep,' in addition to the easy individual mobility afforded by such cities when not in an enforced lockdown and/or curfew, might further facilitate the nocturnal transmission which we hypothesize is primarily driven by evening-oriented individuals.

The similarities between the non-complier profile and the evening-oriented individual profile are salient though not complete. For instance, the personality trait openness to experience is related to eveningness (Lipnevich et al., 2017), but it is not related to non-compliance (Asselmann et al., 2020; Zajenkowski et al., 2020), while agreeableness exhibits no relationship with chronotype (Lipnevich et al., 2017), but has appeared as negatively related to non-compliance (Asselmann et al., 2020; Zajenkowski et al., 2020). Future studies focusing on the Big Five personality traits should be able to settle this point.

We have shown that the chronotype is a relevant aspect of (non)compliance in pandemics and that future studies should explicitly focus on it; however, one may counterargue that it is a mere byproduct of sex, age, and life history strategy. Although sex (i.e., males), age (i.e., young individuals), and life history strategy (i.e., fast life history) tend to exhibit a similar profile to the non-complier, we argue that the eveningness chronotype still holds as an important factor. Indeed, the eveningness chronotype is related to male sex, younger age, and fast life history. Further studies should verify which of those variables maintain a unique relationship with non-compliance when the other variables are co-present as predictors. Evening orientation relates to more facets of non-compliance (e.g., includes extraversion), while some aspects of non-compliance (i.e., wearing face mask) do not show sex differences (Howard, 2020) typical of life history. Importantly, the positive relationship between eveningness and rule-breaking tendency holds independently of sex (Merikanto et al., 2017), and some other traits shared with non-compliant individuals are related to chronotype regardless of sex and/or age (e.g., present orientation/instant gratification, Milfont and Schwarzenthal, 2014; mating orientation, Ponzi et al., 2015b; and Dark Triad personality, Jonason et al., 2013). Moreover, some sex differences expected by life history theory (e.g., sex differences in sensation seeking) only appear in evening-oriented individuals (Antúnez et al., 2014). Furthermore, eveningness matches the time period of social contexts in which there are important superspreading events (e.g., dining restaurants, bars, nightclubs), and matches the period of the day in which the virus is more persistent in the environment.

The more the literature on the new coronavirus pandemic develops, the more certainty we can have about this association and its nuances. There are already many preprints out and more research ongoing, which has not yet been peer-reviewed, and hence, not yet included in our literature review. One study reported that compliance with malaria chemoprophylaxis among soldiers during missions in Africa was negatively associated with eveningness chronotype (OR = 0.68) (Resseguier et al., 2010). Another study found that nighttime curfew indeed decreased the acceleration of the new coronavirus propagation, but mostly among the older population and not among the youngest individuals (up to 19 years old), and not as much as the full lockdown (Baunez et al., 2020). Future studies should directly test the eveningness epidemiological liability hypothesis using correlational and mediational approaches and disentangling the effects of eveningness chronotype from those of sex and age, and potentially even those of fast life history strategy. Until then, we argue that the eveningness chronotype should figure alongside the male sex, younger age, and faster life history strategy (Corpuz et al., 2020) as another crucial factor to be studied in the context of non-adherence to pandemic public safety measures.

The eveningness epidemiological liability hypothesis should not lead to the impression that evening-oriented individuals are always a liability during disease outbreaks (i.e., epidemics and pandemics), nor that night-owls have only negative/undesirable psychological traits. The evening-oriented chronotype also exhibits some desirable features such as intelligence (e.g., Stolarski and Jankowski, 2015; Randler, 2017), openness to experience (Randler et al., 2017), and creativity (Giampietro and Cavallera, 2007), and it is only one of many risk-factors for non-compliance. Moreover, a disease with a different mode of transmission might not be related to chronotype at all. Eveningness is therefore not an *a priori* characteristic of pandemic rule-breaking individuals. Furthermore, some evening-oriented individuals may be healthcare workers and thus can better adjust to the night-time work shift, enabling them to keep saving lives while others cannot function properly (e.g., Silva et al., 2017; Hittle and Gillespie, 2018). However, sleep deprivation interferes with immunity and self-regulation (Shields et al., 2017; Rantala et al., 2021), which might increase the risk of contamination with the new coronavirus, increasing shift workers' vulnerability especially in the healthcare frontline tackling the pandemic (Silva et al., 2020). Thus, not all evening-oriented individuals are a liability or non-compliant with the pandemic safety measures.

The Bigger Picture in COVID-19 Non-Compliance

Far from being the definitive all-encompassing explanation, the eveningness epidemiological liability hypothesis, which focuses more on individual dispositional traits, is only a part of the bigger picture. That is because there are multiple factors in different domains and levels influencing (non)compliance with the health guidelines during the COVID-19 pandemic. Political orientation, such as authoritarianism, is related to low frequency of face mask wearing in public (Prichard and Christman, 2020). Further,

situational and contextual factors also play a role. Situational predictions of non-compliance are: unemployment status, being the woman head of a family, and having less information and low-quality knowledge about COVID-19 (Nzaji et al., 2020). Low exposure to the instructions is also related to non-adherence to safety measures (Pollak et al., 2020), as it is for media diets (Pedersen and Favero, 2020). Some research has even demonstrated that situational factors explained more variance in compliance than dispositional personality traits (Zajenkowski et al., 2020). Most of the abovementioned situational factors—that is, knowledge about the disease and the quarantine, social norms, perceived benefits of quarantine and risks of the disease, lack of supplies, and unemployment—are associated with (non)adherence to quarantine during infectious disease outbreaks (Webster et al., 2020). Moreover, societal norms (loose vs. tight) may also contribute to the varying reactions of world nations in limiting COVID-19 cases and deaths (Seitz et al., 2020; Gelfand et al., 2021). Hence, males, young individuals, those pursuing a fast life history strategy, and evening-oriented individuals are not the only non-compliant type(s); because of situational reasons, many more individuals also end up defying the contagion-mitigating measures. This polymorphic nature of non-compliance suggests public policies should have many profile targets, since "one size fits all" policies are unlikely to be as effective (cf. Arnot et al., 2020). Future studies should always access and control for both dispositional/internal traits (e.g., personality and life history) and situational/external factors (e.g., employment status, marital/relationship status) in order to establish a more comprehensive picture of the phenomenon of non-compliance with virus-mitigating measures (cf. Zajenkowski et al., 2020).

The message is similar regarding superspreading events. The superspreading events emphasized here were all characterized by the "opportunistic" type, in which individuals temporarily cluster in crowded places and sing or speak loudly (Althouse et al., 2020). However, there are other types of superspreading events: the "biological," in which some individuals have an unusually high viral load; the "behavioral/social," in which some individuals have an unusually high number of daily social contacts; and the "high-risk facilities and places," in which individuals are repeatedly exposed to higher potential infection rates such as meat-packing plants, workers' dormitories, prisons, long-term care facilities, or healthcare settings (Althouse et al., 2020). Future studies should sample widely from all those types of events. However, one of the main differences between the opportunistic and the other types is that the former is normally an individual choice done during leisure time, while the others are somewhat more difficult to avoid without imposing extensive societal lockdowns. Therefore, places and contexts in which "opportunistic" superspreading events have occurred are in theory a good target for public communication convincing individuals to avoid those same places during pandemics for safety reasons, or public policy interventions restricting such events altogether.

Further, the methods to quantify non-adherence to public health measures vary across studies and are not yet standardized and validated measures. In the same way that laboratories are rushing to get viable vaccines, other researchers are rushing to create new methods to define and address non-compliance with pandemic health measures. Some studies focus on intentions to follow public health guidelines while others focus on actual or past behavior. Some studies use questionnaires, some use direct observation about actual behavior in public settings, others use GPS data from public cellphones to track individual movements. Some studies focus only on one type of public health safety measure, such as shelter in place, or mask-wearing, while others access a variety of measures from hand sanitizing to avoiding crowded places. The way to define who is non-compliant also varies across studies: some use a histogram-informed cut in the scale used, while others rely mostly on whether people have left home in the last 24 h. This is an expected problem given how recent the pandemic and, consequently, all this related research is. As the second and subsequent waves of the COVID-19 pandemic unfolds (Krams et al., 2021), future studies should invest into unifying and validating measures of non-adherence to pro-health measures in order to promote more comparability among different studies in different places of the world, and to increase certainty about the actual scientific value of each quantitative method employed to study non-compliance with safety measures. A mixed or multi-method approach is also desirable because different methods complement each other in their strengths. Further, a globally distributed collaborative network of laboratories could be decisive to improve the representativeness and the power of studies on pandemic (non)compliance (cf. Moshontz et al., 2018).

Future Research

Nevertheless, we argue that the available evidence stemming from different sources and places around the world is convergent and strong enough to indicate a distinctive pattern: that evening-oriented individuals are probably making a significant contribution to the continuous spreading of the new coronavirus, extending and worsening this pandemic and public health crisis.

Further studies in different populations are needed to establish the veracity of this hypothesis, the size of the effect, and the extent of its validity across different nations and contexts. One possible way of testing the eveningness epidemiological liability hypothesis is checking whether the eveningness chronotype indeed positively correlates with non-compliance with the virus-mitigating health protocols of the current pandemics (e.g., reduced use of shelter in place, no face mask wearing in public, low avoidance of indoor crowded places, etc.), even controlling for sex, age, life history strategy, political orientation, and possibility of home office. In a path analysis design, researchers could test whether any of the following traits, such as paranoia, risk-taking, sensation-seeking and impulsivity, extraversion, lower self-control, promiscuity, aggression, rule-breaking, and dark personality traits act as moderating variables between chronotype and non-compliance. We would predict these traits to be positively correlated with non-compliance. Another possibility is to investigate whether evening-oriented individuals have been infected more frequently by the new coronavirus (i.e., SARS-CoV-2) than morning-oriented individuals. Studies that access cell phone

GPS big data to infer individual mobility can analyze whether places with more nocturnal activities have higher infection rates. Epidemiological studies could compare locations before lockdown with and without night-time curfew to analyse how much of the viral transmission is decreased by impeding nocturnal activities.

Implications for Public Policy

Until then, on the safe side, it is appropriate after careful consideration (IJzerman et al., 2020) to promote security measures that take the crucial sequence of evolutionary mismatches and adaptive metaproblem into account and focus on how to avoid nocturnal individuals from becoming superspreaders while offering secure alternatives for their nocturnal activities. These can include online substitutive activities (e.g., live streams instead of music concerts, social media/video calls instead of in-person socialization, Netflix/movie streaming platforms instead of cinema, online dating instead of flirting in bars, virtual sexual activities instead of in-person intercourse, etc.). Virtual reality technology, which has significant applications in times of COVID-19 pandemic (Singh et al., 2020), also should be used to offer secure social alternatives to evening-oriented individuals.

Our first suggestion is to take chronotype into consideration alongside sex and age as important factors influencing the effectiveness of public communication about pro-health measures. Tailoring the messages to appeal to this psychobehavioral profile could be a very effective strategy; however, caution needs to be taken when applying behavioral research to public policy (IJzerman et al., 2020). In Japan, Nakayachi et al. (2020) discovered that people conformed to societal norms in wearing masks, i.e., the more they heard that most people were using masks, the more willing they became to use them. For instance, one option would be to use this strategy geared toward night-owls, males, and youngsters. Other social psychological and behavioral strategies and techniques (cf. Kantor, 2020; Smith and Gibson, 2020; Van Bavel et al., 2020) might be directed toward predominant evening-types, males, and youngsters in order to minimize viral transmission.

The second suggestion arising from this review is to limit access to those places where evening-oriented individuals normally go during night-time (e.g., bars, nightclubs). Haug et al. (2020) ranked the effectiveness of government non-pharmaceutical interventions worldwide to curb the COVID-19 pandemic: the most effective measures comprised closing and restricting most places where individuals tend to gather in smaller or larger numbers for extended periods of time, such as schools, businesses, and bars. Independently, Brauner et al. (2020) did a similar worldwide analysis and concluded that closing some businesses such as restaurants, bars, nightclubs, cinemas, and gyms had a moderate-to-small effect in reducing COVID-19 transmission, indicating a promising policy option together with limiting gatherings to 10 people or less, which exhibited a large effect in reducing COVID-19 transmission. In France, nighttime curfew indeed decreased the acceleration of SARS-CoV-2 transmission, but the subsequent lockdown was more effective (Baunez et al., 2020). Hence, it seems that a night-time shutdown would indeed inhibit COVID-19 transmission. However, prohibition in some places might also generate clandestine bars and gathering places. Therefore, depending on a low and favorable local transmission rate, some alternative options could remain open, primarily in open air, with good ventilation, in ample spaces, with lower numbers of individuals, all wearing masks. On the other hand, on places where the local transmission rate is rampant due to the new variants of SARS-CoV-2, nighttime curfew is not enough, only a full lockdown, case tracing, and massive vaccination are likely effective.

A consensus reached by a group of experts from the Spanish Association of Sexuality and Mental Health strongly recommended not initiating sexual activity with a sporadic partner during pandemics for safety reasons (Cabello et al., 2020), a recommendation endorsed by Ibarra et al. (2020). Indeed, there has been a decrease in sexual partners, sexual frequency, and sexual risk-taking during the COVID-19 pandemic (Li et al., 2020). Thus, the higher tendency toward casual sex that evening-oriented individuals have can be partially met with virtual sexual activities such as telephone or online sex. This is what the International Society for the Study of Women's Sexual Health (International Society for the Study of Women's Sexual Health [ISSWSH], 2020) recommended since May 2020: the new safe sex is 'e-sex.' Dating apps still allow people to search for new possible partners and flirt safely online. Even those individuals with steady partners who are under quarantine after testing positive for COVID-19, those with some clinical symptoms, those who are pregnant, and those health professionals who are in contact with COVID-19 patients are recommended to abstain from coital/oral/anal sex, substituting it with masturbatory or virtual sexual activity to provide maximum protection against SARS-CoV-2 contagion (Cabello et al., 2020). The dangers inherent in casual sex can create a delicate situation since the life satisfaction of singles has decreased most during COVID-19 lockdowns (Hamermesh, 2020).

Interestingly, there is a growing related literature pointing out that the circadian rhythms which influences gene expression and many cellular and physiological parameters may influence individual susceptibility and resilience to viral infections which interacts with those circadian internal changes (Diallo et al., 2020; Sengupta et al., 2021). Antiviral therapies in COVID-19 patients are more efficient when provided in the morning as opposed to in the evening (De Giorgi et al., 2020), which is presumably independent from individuals chronotype. This circadian rhythm literature, when connected to the findings on the relaxation of social jetlag during the pandemic (e.g., Korman et al., 2020), should be integrated with the non-compliance literature according to the hypothesis presented here for us to be able to have a clear, broad, and deeper understanding of the many ways in which circadian rhythms/chronotype can influence and be influenced by the dynamics of the current COVID-19 pandemic. Chronotype and circadian rhythms are still missing in the discussion about the psychology of pandemics (cf. Taylor, 2019; Ackerman et al., 2020).

CONCLUSION

We have shown a sequence of evolutionary mismatches (**Figure 1**) and an adaptive metaproblem between the context of the evolved psychological profile for nocturnal activities and the compliance with modern pandemic restriction protocols in the context of an infectious respiratory disease outbreak. The main hypothesis put forth in this article is that evolved propensities for nocturnal activities constitute a liability against proper epidemiological control during the current pandemic. Although still lacking key pieces of evidence and being only a part of the bigger picture of non-compliance (cf. Zajenkowski et al., 2020), this hypothesis and its subsequent empirical testing/falsification constitute an important step toward improving public health communication and effectively targeting campaigns to potential superspreaders.

This *eveningness epidemiological liability hypothesis* is substantiated by connecting three main lines of empirical evidence. First, the SARS-CoV-2 is able to persist in aerosols much longer during the night and indoors than during the day outdoors. This sets the stage for the possibility of relatively higher viral transmission and individual contagion during the night. Second, nocturnal activities such as restaurant dining, bars, and nightclubs were identified as contexts of high contamination risk, even originating some superspreading events across-countries (**Figure 2**). This confirms and specifies which night-time places and activities individuals are willingly seeking during their leisure time (i.e., those enabling short-term mating) when they are at an elevated risk of being contaminated or transmitting the new coronavirus. The third line of evidence concerns the psychobehavioral profile comparison between evening-oriented individuals and those non-compliant with public health guidelines (**Table 1**). Importantly, evening-oriented individuals tend to be rule-breakers (Merikanto et al., 2017), which precisely meets the definition of non-compliance with the pandemic safety rules. Both tend to be more frequently males, on average younger, more paranoid, remorseless/antisocial, impulsive, higher in risk-taking, smoking, alcohol use, drug use, extraversion, and short-term mating. These factors are aligned with the fast life-history profile that sexual selection would favor in a nocturnal context of short-term mate search and risky sexual behaviors, but which could maladaptively backfire in a pandemic context of an airborne virus (e.g., Ponzi et al., 2015b; Arnot et al., 2020; Corpuz et al., 2020).

All those same psychobehavioral tendencies amplified in the nocturnal niche throughout human evolution arising via the longstanding habitual use of fire might unfortunately contribute to setting the pandemics 'on fire' via increased transmission rates. This is still a hypothesis that requires a systematic empirical test and should not be used as an excuse to persecute evening-oriented individuals nor to justify enforcing nighttime curfew when the situation requires a full lockdown.

We have developed the eveningness epidemiological liability hypothesis with convergent and empirical evidence (e.g., observational, survey, and cross-cultural studies as well as meta-analyses) stemming from a variety of fields, and based it on a plausible and circumstantiated evolutionary analysis that includes consideration of phylogeny, adaptive challenges, evolutionary mismatches, and adaptive metaproblems.

Without the theoretical foundation presented here, any possible study showing a positive correlation between eveningness and non-compliance would come across as just another correlate of non-compliance among many, and not as a possible core feature of the phenomenon. The evolutionary mismatch hypothesis of eveningness epidemiological liability connects disparate strands of evidence, organizes some of the profusion of recent findings, whilst also helping to guide and focus public health preventive measures. We have presented a broad literature review and a new evolutionarily oriented hypothesis, discussed it against possible alternatives (such as sex, age, and life history) at such length that would not be possible in an empirical research article.

We hope this article can motivate other researchers to improve upon and test this framework comprising four mismatches, an adaptive metaproblem, and the eveningness epidemiological liability hypothesis, serving as a heuristic theoretical and hypothesis-generating review for future confirmatory research. As such, we have made it possible to skip the process of conducting exploratory empirical analyses on the topic and guided researchers straight into doing confirmatory analyses on the framework of this article, which in times of pandemics is desirable given the urgency and severity of the global epidemiological, societal, and economic crises.

DATA AVAILABILITY STATEMENT

This is a purely theoretical contribution, thus there is no data for the authors to make available. The original contribution presented in the study is already included in the article, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

MV conceived and searched the literature and organized and drafted the manuscript. SL, RS, and JV made substantial contributions and reviewed the manuscript critically for intellectual content. MV, SL, RS, and JV revised and approved the final manuscript for submission. All the authors contributed to the article and approved the submitted version.

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Disgust Sensitivity Among Women During the COVID-19 Outbreak

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The emotion of disgust is suggested to be an adaptation that evolved to keep us away from sources of infection. Therefore, individuals from populations with greater pathogen stress should have a greater disgust sensitivity. However, current evidence for a positive relationship between disgust sensitivity and the intensity of infectious diseases in the environment is limited. We tested whether disgust and contamination sensitivity changed in response to the COVID-19 pandemic. Disgust was assessed in 984 women in 2017 (before pandemic) and 633 women in 2020 (during pandemic) by a set of photographs depicting sources of infection and Pathogen and Moral of Three-Domain Disgust Scale. Further, contamination sensitivity among participants in two waves was measured by Contamination Obsessions and Washing Compulsions Subscale of Padua Inventory. State anxiety was measured with the Polish adaptation of the State-Trait Anxiety Inventory (STAI) only during the second wave of data collection. Women from the COVID-19 pandemic group assessed the photographs depicting sources of infection as more disgusting, scoring higher on Padua Inventory, but lower on Moral Disgust Domain as compared to women from before the pandemic. In addition, anxiety levels during pandemic positively correlated with scores from Pathogen Disgust Domain, Padua Inventory, and the ratings of the photographs. The participants of the study scored higher in state anxiety than the norms determined for the Polish population. Summarizing, we present evidence for differences in individual levels of disgust sensitivity in relation to pathogen stress, supporting the idea that disgust evolved to serve as protection from pathogens.

Keywords: COVID-19 pandemic, aversion, pathogen stress, evolutionary psychology, behavioral immune system

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INTRODUCTION

Disgust, a universal human emotion, is elicited by a number of factors, including the sources of potential pathogens, such as bodily fluids, people with visible symptoms of disease, dirty environments, rotting food, certain animals, or the violations of moral norms, and antisocial behaviors, including cheating and stealing (Darwin, 1872; Brown, 1991; Curtis and Biran, 2001). The facial expression of disgust (wrinkling of the nose, pulling down the corners of the mouth) is recognizable across cultures (Mesquita and Frijda, 1992). Disgust may be accompanied by strong physical reactions, such as galvanic skin responses, lowered blood pressure, and nausea (Rozin et al., 1993). Pathogen disgust motivates the avoidance of infectious pathogens and is the first line of defense against pathogens (Wicker et al., 2003; Oaten et al., 2009; Stevenson et al., 2009, 2011; Tybur et al., 2009; Curtis et al., 2011). Moral disgust, on the other hand, serves the purpose of avoiding social norm violations (Tybur et al., 2009; Curtis, 2011).

People vary in the degree to which they experience disgust toward pathogens cues. Research concerning behavioral immune system has suggested that greater infection-avoiding behavior and attitudes might be triggered by the presence of infection cues and by one's intrinsic vulnerability to infection. It has been suggested that pathogen avoidance motivation may promote health and longevity by allowing for lower levels of non-targeted inflammation without an increase in infection risk (Gassen et al., 2018). Hence, disgust may be one mechanism that helps people effectively manage such threats, where highly disease-avoidant people bear lower infection costs (e.g., Gassen et al., 2018; Cepon-Robins et al., 2021).

Another line of inquiry suggests that disgust sensitivity is shaped by earlier exposures to pathogens (Tybur et al., 2018), and that it is higher in people who are relatively more vulnerable to infectious diseases (Schaller, 2011). Studies have shown higher anxiety among patients with rheumatoid arthritis toward infection-risky behaviors (Oaten et al., 2017) and heightened attention to and avoidance of individuals displaying disease cues among recently ill people (Miller and Maner, 2011). Moreover, it has been suggested that not only decreased ability to avoid illness might alter disgust sensitivity, but priming disease cues also might upregulate disgust (e.g., Curtis et al., 2011). Thus, people might functionally upregulate disgust during the pandemic to manage ongoing infection threats (Skolnick and Dzkoto, 2013; Ackerman et al., 2021; Stevenson et al., 2021). Summarizing, a degree to which people are disgusted by pathogen cues should depend on pathogen stress, and, consequently, on the risk of getting infected.

However, current evidence for the positive relationship between pathogen stress and disgust level in humans is limited. Attempts to compare disgust across a number of nations that vary in pathogen stress have led to inconclusive results (Curtis et al., 2011; Skolnick and Dzkoto, 2013; Tybur et al., 2016; Ackerman et al., 2021; Stevenson et al., 2021). Based on this there might be no relationship between current infection burden and pathogen disgust (Curtis et al., 2011; Tybur et al., 2016). Comparing different nations, however, is biased due to the fact that disgust sensitivity may be influenced by culture-specific factors, for example, cultural ideas of purity and pollution. Other attempts to demonstrate that disgust sensitivity and pathogens are connected focused on differences in individual disgust sensitivity and illness frequency (Stevenson et al., 2009), history of infectious diseases in childhood (de Barra et al., 2014), or general health (Prokop et al., 2010; Prokop and Fančovičová, 2011). However, the results of these studies fell short of being conclusive. For example, no effect of illness recency on attentional bias for disfigured faces was found in a replication of Miller and Maner's (2011) study (Tybur et al., 2020). It has been also shown that decreased ability to avoid infections downregulates rather than upregulates disgust (Bartres and Perrett, 2020; Cepon-Robins et al., 2021).

Since December 2019, an outbreak of respiratory disease caused by a new strain of coronavirus (SARS-CoV-2) has spread rapidly throughout the world, dramatically increasing pathogen stress in many countries. The dramatic change in the prevalence and virulence of pathogens in the environment during the COVID-19 pandemic created unique conditions for testing the relationship between the level of disgust and pathogen stress within a single population. If disgust, indeed, serves as a first line of defense against pathogens, people should show greater pathogen disgust during a pandemic than during a time of lower pathogen stress. To this date only Stevenson et al. (2021) have shown that university students during Australia's COVID-19 pandemic lockdown period reported higher disgust sensitivity, while comparing to earlier student cohorts. In this study, we aim to test whether there is a difference in disgust sensitivity level between the data collected in year 2017—before the COVID-19 pandemic—and during the pandemic in 2020.

Abbreviations: STAI, State-Trait Anxiety Inventory.

MATERIALS AND METHODS

Participants

In 2017 (before the COVID-19 pandemic) we recruited 984 women and in 2020 (during the COVID-19 pandemic) −633 women. All the participants were Poles, aged 18–45. All women completed at least one questionnaire on disgust level. The first wave of data was collected in 2017 as part of a study that examined relations between disgust sensitivity and menstrual cycle phases in women (Miłkowska et al., 2019). In March 2020, Polish government introduced special restrictions due to the growing number of COVID-19 cases, including social distancing, closing of state borders, schools, cinemas, most stores, and restricting the number of people in churches. The 2020 sample was selected to match the first round of data collection, both in terms of the methods used and the sample size. A sensitivity analysis revealed that the sample size of 1,617 allowed us to detect a small effect size of $\eta_p^2 = 0.004$.

Procedure

The research was conducted in two rounds: before the COVID-19 pandemic in May and June 2017, and during the COVID-19 pandemic in April and May 2020. The data was collected using the same protocol during both waves. Information about the study and invitation to participate were published in social media e.g., on Facebook through the fanpages of Polish women's magazines, e.g., Women Health's and advertised as a "Study on disgust in women." Women were not compensated for participation. The surveys were available in the Polish language for participants at: www.qualtrics.com (before the COVID-19 pandemic) and at: www.limesurvey.org (during the COVID-19 pandemic).

The first part of the survey included questions about health and selected demographic information, and the second part of the survey consisted of questions about disgust sensitivity and experiencing anxiety. Informed consent was obtained from all participants of the study.

Measures

Disgust

Disgust sensitivity in women was assessed by set of photographs depicting sources of infection (Curtis et al., 2004) and two of three

domains of Three-Domain Disgust Scale (Pathogen Disgust and Moral Disgust Domains; Tybur et al., 2009).

The women assessed the intensity of their disgust feelings while looking at each of 20 photographs (Curtis et al., 2004). Women assessed each picture on a 5-point Likert-type scale where 1 stood for "not disgusted" and 5 for "very disgusted." The analyses included ratings of only seven photos that showed potential source of infections, such as: a person looking feverish and spotty-faced, inside of a crowded underground train, a skin lesion with pus and inflammation, a plate of viscous liquid resembling bodily fluids, stained towel with reddish-yellow bodily secretions, louse, and ascaris worms.

Additionally, the participants answered seven questions from Pathogen Disgust Domain and seven from Moral Disgust Domain of TDDS (Tybur et al., 2009). The third domain—Sexual Disgust Domain—was not included in the first wave of data collection, as it is usually not used in research on disgust sensitivity across menstrual cycle (Zelazniewicz et al., 2016; Miłkowska et al., 2019). The questions in Pathogen and Moral Domains concerned the level of disgust toward hypothetical situations e.g., seeing a cockroach run across the floor, shaking hands with a stranger who has sweaty palms, shoplifting a candy bar from a convenience store, or intentionally lying during a business transaction. The items of questionnaire were scored on a 7-point Likert-type scale ranging from "not at all disgusting" (1) to "extremely disgusting" (7). The higher a woman scored in both questionnaires, the higher disgust sensitivity she exhibited.

Contamination Sensitivity

The level of contamination sensitivity was also measured twice among two groups of women. The participants answered questions from Contamination Obsessions and Washing Compulsions Subscale of Padua Inventory—Washington State University Revision (Burns et al., 1996). We used a 5-point Likert-type scale ranging from "not at all" (1) and "very much" (5) e.g., "I feel my hands are dirty when I touch money."

Anxiety

State anxiety was measured only during the second wave of data collection with the Polish adaptation of the State-Trait Anxiety Inventory's (STAI) subscale dedicated to measure anxiety defined as subjective transitory feelings of angst and tension (Spielberger et al., 1970; Sosnowski et al., 2011). The state anxiety STAI subscale consists of 20 items (e.g., I feel calm; I feel secure; I feel tense) rated on a Likert-type scale with higher scores indicating greater anxiety level.

Statistical Methods

Preliminary analyses compared groups of women participating in the study before and during the COVID-19 pandemic in age (by the *t*-test) and in occupation status and long-term health problems (by the chi-squared test). The pre-pandemic and pandemic groups did not differ with regard to occupation status [$\chi^2_{(1)} = 0.640$, $p = 0.423$], belonging to professions connected to potential disgust elicitors (i.e., involving contact with dirt, animals, body secretions, animal, or human tissue) [$\chi^2_{(1)} = 0.039$, $p = 0.843$], or having long-term health problems (lasting longer than 12 months) [$\chi^2_{(1)} = 0.021$, $p = 0.883$]. The groups of women differed in mean age: those who took part in the study in 2020 were about 1 year older (mean = 27.7, $SD = 6.60$) than those from the 2017 group (mean = 26.6, $SD = 5.95$) [$t_{(1615)} = -3.261$, $p < 0.001$] (**Table 1**).

Since the groups of women slightly differed in age, all the differences in disgust sensitivity between them were subjected to analyses of covariance (ANCOVA), with age as a potential confounder. Moreover, a linear regression was used to analyze the correlation between disgust sensitivity and STAI. State-Trait Anxiety Inventory scores were also converted to standardized "Standard Ten" (sten) scores in order to compare anxiety levels in study sample with the norms determined for the Polish population. A sten score reflects individual's position relative to other people from the population of reference. "Standard Ten" scale ranges from 1 to 10 with a mean value of 5.5 and standard deviation of 2. In psychometric assessments calculating

TABLE 1 | The comparison of women from COVID-19 pandemic and pre-pandemic groups with respect to their age (*t*-test), occupation, profession connected to disgust elicitors, and long-term health problems (chi-squared).

	Before COVID-19		During COVID-19				
Variable	**Mean**	**SD**	**Mean**	***SD***	***t***	***df***	***p***
Age	26.6	5.95	27.7	6.60	**−3.261**	**1615**	**<0.001**
	n	**%**	***n***	**%**	**χ^2**	**df**	**p**
Occupation							
Yes	564	57.32	350	55.29	0.640	1	0.423
No	420	42.68	283	44.71			
Profession connected to disgust elicitors*							
Yes	118	11.99	78	12.32	0.039	1	0.843
No	866	88.01	555	87.68			
Long-term health problems							
Yes	301	30.84	194	31.19	0.021	1	0.883
No	675	69.16	428	68.81			

**Profession involving contact with dirt, animals, body secretions, and animal, or human tissue. Statistically significant results are in bold.*

TABLE 2 | Disgust sensitivity among women—the comparison of groups of women from COVID-19 pandemic and pre-pandemic groups after controlling for age.

		n	Adj mean	*SE*	*F*	*P*	η_p^2
Photographic stimuli (mean score)	Before COVID-19	942	3.33	0.02	**433.82**	**<0.001**	**0.220**
	During COVID-19	597	4.19	0.04			
Padua inventory	Before COVID-19	966	2.37	0.03	**38.417**	**<0.001**	**0.024**
	During COVID-19	613	2.61	0.04			
Moral disgust	Before COVID-19	942	5.22	0.04	**6.276**	**0.012**	**0.004**
	During COVID-19	597	5.11	0.05			
Pathogen disgust	Before COVID-19	984	4.71	0.04	0.551	0.458	<0.001
	During COVID-19	633	4.66	0.04			

Statistically significant results are in bold.

TABLE 3 | Relationship between disgust sensitivity and state anxiety (State-Trait Anxiety Inventory).

	n	*β*	*SE*	*p*
Photographic stimuli (mean score)	584	0.13	0.003	**<0.001**
Padua inventory	584	0.16	0.04	**<0.001**
Moral disgust	584	0.03	0.79	0.431
Pathogen disgust	584	0.10	0.03	**0.012**

Statistically significant results are in bold.

raw questionnaire scores to sten scores is a standard practice. All statistical analyses were performed in STATISTICA 13.3 and JASP (Version 0.11.1; JASP Team, 2019).

RESULTS

As compared to the participants from the pre-pandemic group the women who took part in the study during the COVID-19 pandemic assessed the photographs depicting the sources of infection as more disgusting [$F_{(1,1537)} = 433.82$, $p < 0.001$], and scored higher on the Contamination Obsessions and Washing Compulsions Subscale of Padua Inventory [$F_{(1,1576)} = 38.42$, $p < 0.001$]. Moreover, they had lower scores in Moral Disgust Domain than the pre-pandemic group [$F_{(1,1614)} = 6.28$, $p = 0.012$]. There were no statistically significant differences in Pathogen Disgust Domain among these two groups [$F_{(1,1614)} = 0.551$, $p = 0.458$] (**Table 2**).

Among women participating in the study during the COVID-19 pandemic, anxiety (measured by STAI questionnaire) positively correlated with scores from Pathogen Disgust Domain ($\beta = 0.10$, $p = 0.011$), the Padua Inventory ($\beta = 0.16$, $p < 0.001$), and the ratings of the photographs ($\beta = 0.13$, $p < 0.001$). However, the correlation between scores from STAI and Moral Disgust Domain was not statistically significant ($\beta = 0.03$, $p = 0.431$; **Table 3**). The participants of the study also scored 0.36 stens higher in state anxiety than the population of reference, and this difference was statistically significant ($t = 3.33$, $df = 583$, $p < 0.001$).

DISCUSSION

Our results of the comparison of disgust sensitivity and contamination sensitivity between two groups of women characterized by similar demographics during time periods characterized by a different pathogen stress level supports the idea that disgust as a behavioral adaptation is the first psychobehavioral line of defense against pathogens. As compared to the women from before the COVID-19 outbreak the group from the time of the COVID-19 pandemic assessed the photographs of sources of infection as more disgusting, and scored higher on the Contamination Obsessions and Washing Compulsions Subscale of Padua Inventory, but not on Pathogen Disgust of Three-Domain Disgust Scale. The observed difference was most pronounced in the case of response to visual stimuli (effect size $\eta_p^2 = 0.220$). Significantly, some researchers have suggested that visual methods of measurement (including measurement of reaction time) provide the most objective method of assessing the mechanisms of pathogen disgust (Miller and Maner, 2011; Ersche et al., 2014). Hence, as we hypothesized, when the environment becomes more dangerous through increased exposure to infections, people enhance their disgust sensitivity.

Our results are partially consistent with Stevenson, Saluja and Case (2021) study on the impact of the COVID-19 pandemic on disgust sensitivity, using a different population and measures. Students during Australia's lockdown period of the COVID-19 pandemic reported overall higher levels of disgust sensitivity and higher scores for Core Disgust subscale from revised version of Disgust Scale (Olatunji et al., 2009), which is most similar to the Pathogen Disgust of Three-Domain Disgust Scale used in our study. Interestingly, while Stevenson et al. (2021) found evidence for differences in self-reported disgust scale answers in a mixed-sex population of college students in Australia, we found evidence for a difference in disgust sensitivity using a naturalistic measure (the photographs of infection sources) but not a self-report scale with a sample of women from Poland. Stevenson et al. (2021) also provided some evidence of an increase in germ aversion and an increase in hand and food-related hygiene.

Further, our results are also in line with Skolnick and Dzkoto (2013), who found a higher level of disgust sensitivity in a country with relatively high pathogen stress (i.e., Ghana), as compared to a country of relatively low parasite stress (i.e., USA). However, other studies have shown a lack of differences in the level of disgust among participants from countries with different infectious disease rates (Tybur et al., 2016), and in disgust ratings of photographs across nine world regions (e.g., Europe, the Far East, North America, Latin America, the Indian Subcontinent,

and the Eastern Block; Curtis et al., 2011). However, comparing disgust sensitivity in different nations can be problematic not only due to cross-cultural variation in food preferences, hygiene norms, and taboos (e.g., Sherman and Billing, 1999; Navarrete and Fessler, 2003), but also due to the population's variation in genetic mutations conferring resistance to infectious diseases (e.g., Prugnolle et al., 2005; Fumagalli et al., 2009).

The studies that focused on differences in individual levels of disgust sensitivity in relation to health status in a single population are limited, and provide inconclusive results. On the one hand, stronger emotions, which should protect against infections, correlated with better health. Higher disgust sensitivity was associated with fewer recent infections (Stevenson et al., 2009), lower infection burden (e.g., Gassen et al., 2018; Cepon-Robins et al., 2021), and pathogen avoidance behaviors were more frequently reported by healthy people (Prokop and Fančovičová, 2011). Moreover, a childhood illness and, to a lesser extent, a recent illness were associated with perceived infectability (Makhanova et al., in press). However, other studies indicated that higher fear and disgust were associated with worse health. For example, higher fear of disease-relevant animals was found in participants with lower self-perceived health (Prokop et al., 2010); the level of disgust with ectoparasites positively correlated with a total number of reported illnesses (Prokop and Fančovičová, 2011); and higher contamination sensitivity was associated with more frequent infectious illnesses (Stevenson et al., 2009). Furthermore, some studies failed to find any relationships between disgust sensitivity and health. A study by de Barra et al. (2014) showed a lack of relationship between having more infectious diseases in childhood and greater adult disgust sensitivity. Oaten et al. (2017) demonstrated that disgust sensitivity did not differ between people with rheumatoid arthritis (increasing the risk of infection-related morbidity and mortality) and healthy controls. It should be noted, however, that none of these studies addressed actual pathogen stress exposure.

Another finding of our study is related to the Moral Disgust Domain. During the COVID-19 pandemic the women had lower moral disgust scores than before the pandemic. It has been suggested that many traditions, rituals, religious beliefs, and moral norms historically helped to prevent infectious diseases (Fabrega, 1997). Therefore, people under high pathogen stress should respond especially harshly to norm violations. For example, it has been shown that individuals in nations with greater parasite stress reported stronger adherence to traditional norms (Tybur et al., 2016). At the individual level, some studies suggested that experienced disgust triggered by, for example, exposure to a bad smell ("fart spray"; Schnall et al., 2008), drinking bitter liquid (Eskine et al., 2011), or watching a revolting clip (the toilet scene from *Trainspotting*; Schnall et al., 2008) can increase the severity of moral judgments. However, other studies failed to replicate these results (i.e., Schnall et al., 2008; Ugazio et al., 2012; Johnson et al., 2014). Therefore, the role of disgust, triggered by potential infection sources, for moral judgment is still unclear (for review see Landy and Goodwin, 2015). Horberg et al. (2009) suggested that higher disgust sensitivity might be positively related to stronger condemnation of behaviors violating purity (consensual incest; having sex with a dead chicken prior to consuming it), but not with punishment of justice transgressions (not returning an important library book; interrupting meetings to ask for small favors).

It should be noted that the Moral Domain in the Three-Domain Disgust Scale used in our study does not pertain to any purity transgressions (Tybur et al., 2009). The questions relate only to justice and loyalty validation (e.g., deceiving a friend, stealing from a neighbor, lying during a business transaction, shoplifting a candy bar, forging someone's signature on a legal document). Thus, it is possible that in our study the women who participated during the COVID-19 pandemic were less disgusted by behaviors that in a time of reduced wages, supply shortages, and economic uncertainty might help in self-preservation and the assurance of financial security.

We also observed significant associations between the scores of state anxiety and the Pathogen Disgust in the Three-Domain Disgust Scale, the Contamination Obsessions and Washing Compulsions Subscale of the Padua Inventory, and the ratings of photographs of sources of infection. These results are consistent with studies reporting associations between disgust sensitivity and anxiety related to potential health hazards (Fan and Olatunji, 2013). Further, as Stevenson et al. (2021) suggested, the level of threat that people perceive during the COVID-19 pandemic might be far higher than normal, which could in turn increase the intensity of disgust sensitivity. For instance, in a study on psychological processes associated with the Ebola outbreak in the 2014, the fear of the disease was associated with increased general distress, body vigilance, and disgust sensitivity (Blakey et al., 2015). We did not, however, observe similar correlations between state anxiety and moral disgust, which suggests that moral disgust is associated with different psychological mechanisms, and is to a lesser extent driven by anxiety.

One of the limitations of the study design was the lack of the possibility to compare the disgust sensitivity of the same women before and during the COVID-19 pandemic. We are fully aware of the bias related to between-subject design, including the confounding effect of inter-individual differences. However, such data is much more difficult to collect, especially in a pandemic context. In contrast to previous studies we did not compare different nations (Curtis et al., 2011; Skolnick and Dzkoto, 2013; Tybur et al., 2016), but two large groups of women from the same country under changed environmental conditions. The groups did not differ in any factors that could influence their perception of disgust (i.e., occupational status, long-term health problems, or belonging to professions connected to potential disgust elicitors). A further limitation is that we compared ratings only in groups of women. However, as reported before, disgust sensitivity varies consistently between men and women, with higher scores on measures of disgust sensitivity in women than men (Haidt et al., 1994; Rozin et al., 1999; Curtis et al., 2004). Moreover, in our study we tested only differences in disgust sensitivity and contamination sensitivity. Hence, future studies concerning this topic would benefit from analyzing both women and men, using a longitudinal study design, and including a wider range of emotions.

In our study it was documented that the participants from the pandemic group assessed the photographs of infection sources as more disgusting, but they did not show any increase in the Pathogen Disgust of the Three-Domain Disgust Scale. This lack of differences might be caused by the characteristics of the questionnaire, which was criticized by Fleischman and Fessler (2018), and by Tybur et al. (2016) as potentially insensitive in pathogen avoidance motivations. Self-reported disgust with graphic visual images containing disease cues has been proposed as a more sensitive and accurate measure of pathogen disgust sensitivity than a self-reported disgust for text-only questionnaire items (Fleischman and Fessler, 2018).

Summarizing, we present a comparison of disgust level and contamination sensitivity in two groups of women characterized by similar demographics during two time points when pathogen stress varied. The outbreak of the COVID-19 pandemic provided an opportunity to compare the population's samples from two different pathogenic environments. Our results, indicating higher level of disgust sensitivity during the COVID-19 pandemic compared to pre-pandemic period, support the idea that disgust evolved to serve as a form of protection from pathogens.

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 Jagiellonian University Ethics Committee. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

KM, AG, and GJ designed the study. KM collected the data. KM, MM, and AG performed statistical analyses. All authors participated in writing a first draft of the paper, editing the manuscript, contributed to the article, and approved the submitted version.

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BRIEF RESEARCH REPORT
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COVID-19 Protective Behaviors Are Forms of Prosocial and Unselfish Behaviors

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The aim of this study was to explore the effects of prosocial and antisocial personality tendencies and context-related state factors on compliance with protective behaviors to prevent the spread of coronavirus infections. Six types of prosocial tendencies (altruism, dire, compliant, emotional, public, and anonymous) and selfishness as the antisocial tendency were included as personality factors, while fear related to the pandemic and empathy toward vulnerable groups (i.e., those in forced isolation) were context-related factors. Furthermore, mediation effect of empathy and moderation effect of fear were explored in relations between personality factors and protective behaviors. The sample included 581 participants (78.3% females). The data were collected from March 28 to April 6, 2020, during the emergency state and curfew in Serbia. The results showed that tendency to help anonymously had a positive effect and selfishness had a negative effect on protective behaviors, over and above demographic characteristics and context-related factors. Among context-related factors, only fear related to the pandemic had a significant unique positive effect on protective behaviors, but it had no moderator effect in the relationship between personality traits and protective behaviors. However, empathy acted as a mediator and partly accounted for the negative effect of selfishness and positive effect of tendency to help anonymously on protective behaviors. The results revealed that compliance with protective measures could be seen as prosocial and unselfish form of behavior. Furthermore, these findings have practical implications for shaping public messages and they can help effectively promote health-responsible behaviors.

Keywords: COVID-19, coronavirus, protective behaviors, selfishness, prosociality, empathy, fear

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INTRODUCTION

In order to contain the spread of COVID-19 infections, the World Health Organization proclaimed several protective measures, such as physical distancing, wearing a mask, avoiding crowds, and cleaning hands (World Health Organization, 2020). These protective behaviors that serve to keep a person safe and protected from the virus infection could also be seen as prosocial behaviors. For example, by wearing a mask and keeping a physical distance, people protect others, especially those most vulnerable to the virus, such as the elderly and individuals with respiratory problems. However, in a review of evolutionary insights into the understanding of the pandemic's impact on human behavior, Seitz et al. (2020) stated that it was unclear whether protective behaviors referred to cooperative motives and solidarity among people or to concerns about oneself and close family members and worries about social shaming and legal sanctions.

From the standpoint of evolutionary psychology, the main goal of individual behaviors is the pursuit of survival and reproduction (Buss, 2019). Our behaviors are consequences of successful problem-solving strategies of our ancestors who passed down these adaptive behaviors to subsequent generations. However, strategies for securing resources can vary. There are two kinds of strategies that have evolved, prosocial and antisocial (e.g., Gilbert and Basran, 2019). The prosocial strategy can help in providing resources and securing reproductive opportunities by ensuring mutual advantages in terms of breeding, offspring care, and a cooperative alliance. The antisocial strategy includes competition for resources, both within and between groups, in an environment in which only the strongest wins. Thus, in the global crisis of the COVID-19 pandemic, the question is which strategy underlies protective behavior. On the one hand, there is the long-held popular view that human nature is inherently self-serving and selfish. However, challenging contexts, such as the COVID-19 pandemic, may actually promote altruism (Vieira et al., 2020). Prosocial behaviors could be driven by altruistic motives focused on maximizing others wins or egoistic motives focused on maximizing own wins. In this study six types of prosocial tendencies were explored and they ranged from self-oriented (i.e., public prosociality as a tendency to perform prosocial acts in front of an audience, motivated by the desire to gain the approval of others) to other-oriented (i.e., altruistic and anonymous prosociality as a tendency to perform prosocial acts without knowledge of whom helped, see Carlo and Randall, 2002).

Previous research has yielded mixed results about the prosocial correlates of compliance with protective behaviors. For example, Pfattheicher et al. (2020) showed that empathy was related to physical distancing and wearing a mask, while inducing empathy for people most vulnerable to the virus promoted the motivation to adhere to protective behaviors. Greater empathy toward vulnerable others along with greater perception of social cohesion significantly predicted support for protective measures (Böhm et al., 2020). Furthermore, the motivation to engage in protective behaviors was increased by public health appeals more than by personal health appeals (Jordan et al., 2020).

However, other authors reported no significant relation between altruism and some protective behaviors, such as social distancing (Sheth and Wright, 2020). Moreover, Nakayachi et al. (2020) investigated the reasons for wearing a mask among the Japanese and found that the perceived self-efficacy of wearing a mask in reducing personal infection risk had a higher correlation with mask usage compared to the reduction of risk for others. However, both reasons still had negligible effects in the prediction of mask usage (Nakayachi et al., 2020). The most prominent predictor for wearing masks was conformity to the social norms, followed by the feeling of relief from anxiety (Nakayachi et al., 2020). Compliance with protective measures has been one of the main themes in papers related to fear and anxiety triggered by COVID-19 (Coelho et al., 2020). In the context of prosocial behaviors, fear, anxiety, and personal distress force individuals to focus on their own emotions and personal losses as opposed to others' gains (Paciello et al., 2013). Consequently, they motivate people to act in a self-interested manner, i.e., to ensure personal survival. Many studies have confirmed the link between personal fear of COVID-19 and protective behaviors (e.g., Harper et al., 2020). However, in some studies, the measure of worry about the consequences of the novel coronavirus was not separated from worry for oneself, family, and close friends, but the overall score on worry showed a substantive positive correlation with protective behaviors across different countries (Jørgensen et al., 2020). Therefore, fear of the pandemic should be taken into account as a strong context-related state factor in the explanation of compliance with protective measures.

In answering the question of whether prosocial or antisocial tendencies could explain compliance with protective measures, previous studies that included basic personality traits also showed mixed results. Among the Big Five traits, the trait related to prosociality, empathy, and helping behavior is Agreeableness (Graziano et al., 2007). While the majority of studies reported positive relations between Agreeableness and protective behaviors during the pandemic (Aschwanden et al., 2020; Blagov, 2020; Bogg and Milad, 2020), some studies did not find significant relations (Shook et al., 2020), or they found even negative relations (Abdelrahman, 2020). In the context of the HEXACO personality model, Honesty-Humility reflects active cooperation, the tendency to cooperate with others despite the opportunity for exploitation, while Agreeableness reflects reactive cooperation, the tendency to cooperate with others despite their misgivings (Ashton et al., 2014). However, meta-analysis showed that only Honesty-Humility was related to prosociality and not Agreeableness from the HEXACO model (Thielmann et al., 2020). In the same vein, previous research has found Honesty-Humility, but not Agreeableness, to be positively related to support for limited social gatherings and the closing of restaurants (Böhm et al., 2020). Similar, (Zettler et al., 2020) showed significant effect of Honesty-Humility on distancing, while Agreeableness had no significant effect on both distancing or hygiene, although both traits showed significant correlations with those protective behaviors. Conversely, the constellation of socially aversive traits known as the Dark Triad has been consistently linked to non-compliance with protective measures (e.g., Nowak et al., 2020; Triberti et al., 2021; Zettler et al., 2020). Dark Triad traits refer to antisocial strategies that share common characteristic of manipulativeness and lack of affective responsivity or empathy (Dinić et al., 2020). Furthermore, one of the core elements of this constellation could be selfishness (Diebels et al., 2018). Additionally, Moshagen et al. (2018, p. 656) defined the common core of dark traits or D factor as "the tendency to maximize one's individual utility-disregarding, accepting, or malevolently provoking disutility for others-, accompanied by beliefs that serve as justifications" which also refers to selfishness. However, prosocial and antisocial tendencies are not merely opposite sides of the same dimension. Rather, they form related but distinct constructs (e.g., Krueger et al., 2001). Thus, it seems important to include both prosocial and antisocial tendencies as predictors in explorations of the nature of protective behaviors.

The main aim of this research was to explore the effects of specific personality traits and tendencies related to prosociality (prosocial tendencies) and antisociality (selfishness) along with

the effects of context-related factors (fear related to the pandemic and empathy toward people in forced isolation) on compliance with protective measures. Previous research suggested that context-related factors were more important and outperform the personality traits in explanation of protective behavior (e.g., Zajenkowski et al., 2020). However, other research suggested the important role of personality traits (Zettler et al., 2020). Additionally, previous research suggested that demographic characteristics need to be considered in exploration of protective behaviors (e.g., Lüdecke and von dem Knesebeck, 2020). Therefore, in order to gain insight into the main characteristics of protective behaviors and determine whether they reflect prosocial or selfish tendencies, compared to previous research (e.g., Blagov, 2020), we explored the effects of personality traits in the explanation of compliance with protective measures over and above context-related factors and demographics. In this way we controlled the effects of context-related factors and demographics in relations between prosocial and antisocial tendencies and protective behaviors. We expected that the practice of protective behaviors would be positively affected by other-oriented prosocial tendencies (such as altruism) and negatively affected by selfishness and self-oriented prosocial tendencies (such as public prosocial tendency).

The second aim was to explore the mediation and moderation role of context-related factors in relations between personality traits and protective behaviors. Most studies have confirmed the strong relation between protective behaviors and empathy, especially toward the vulnerable ones (e.g., Pfattheicher et al., 2020). Since antisocial or "dark" tendencies are negatively linked to empathy (e.g., Dinić et al., 2020), we expected selfishness and self-oriented prosocial tendencies to be negatively related to protective behaviors due to a lack of empathy, i.e., that empathy acts as a mediator. Conversely, we expected that positive effects of other-oriented prosocial tendencies on protective behaviors could be explained by higher empathy. In the case of fear, we assumed that it could act as a moderator. Namely, fear of COVID-19 appears to be a strong correlate of protective behaviors (e.g., Coelho et al., 2020). However, there are no theoretical arguments for relations between prosocial and antisocial tendencies and fear related to pandemic. Although we expected that selfishness and self-oriented prosocial tendencies decrease protective behavior, if the fear is high among those with higher selfishness and self-oriented prosocial tendencies, we assumed that it would lead to higher compliance with protective measures. In the same vein, we expected that a positive link between other-oriented prosocial tendencies and protective behaviors would increase in the case of higher fear.

METHOD

Participants and Procedure

The sample included 581 participants (78.3% females) from Serbia, aged between 19 and 72 ($M = 34.01$, $SD = 10.27$). The majority of participants were highly educated (50.8% university graduates, 10.3% university postgraduates or PhD students, 21.7% students, and 6.0% finished college), while 11.2% finished primary or secondary school. Participants reported 1 (meaning they lived alone) to 12 household members. Due to the small frequencies of participants in households with more than 6 members, these answers were merged into one category ($M = 3.06$, $SD = 1.34$).

Participants were invited to take part in the study through a social media announcement. The data were collected from March 28 to April 6, 2020 (the 2nd and the 3rd week of the emergency state in Serbia). The study was a part of a larger research project, which was approved by the Ethical Committee of the Department of Psychology, Faculty of Philosophy, University of Novi Sad, Serbia, which is the Second Instance Commission of the Ethical Committee of the Serbian Psychological Society (No. 202003221959_nytc). A part of the data was also used in Dinić and Bodroža (2020).

Instruments

The COVID-19 Protective Behaviors Scale was developed for the purpose of this study. It contains 9 items (e.g., washing hands, wearing a mask, wearing sanitary gloves, and physical distancing) with a 5-point Likert scale for the frequency of each behavior (from 0 = never to 4 = all the time). Based on the principal axis method, only one factor had an eigenvalue over 1 ($\lambda = 3.08$), which explained 24.26% of the common variance. Factor loadings ranged from 0.36 ("consciously prevent yourself from touching your face with your hands when you are outside") to 0.74 ("disinfect your shoes when you get home"). The mean score was 3.63 ($SD = 0.87$) and the alpha was 0.82.

The Empathy Toward Persons in Forced Isolation Scale was developed for the purpose of this study. It contains 6 items (e.g., "I get very sad when I think of people who are forced into total isolation.") with a 5-point scale (from 1 = never to 5 = always). Based on the principal axis method, only one factor had an eigenvalue over 1 ($\lambda = 2.44$), which explained 40.66% of the common variance. Factor loadings ranged from −0.41 ("Talks and messages about helping people in isolation irritate me.") to 0.77 ("I am thinking about people who are in forced isolation and the situation in which they are.").

The Fear scale from the Positive and Negative Affect Schedule (PANAS; Watson et al., 1988, for the Serbian adaptation see Mihić et al., 2014) contains 5 items. Participants were asked to judge on a 5-point scale (from 1 = *not at all* to 5 = *very much*) how they felt since the COVID-19 pandemic started in Serbia.

The Selfishness Questionnaire (SQ; Raine and Uh, 2019, for the model fit of the Serbian adaptation see Dinić and Bodroža, 2020) contains 24 items with a 5-point scale (from 1 = *strongly disagree* to 5 = *strongly agree*) that measure adaptive (selfish acts with benefits for oneself and close persons such as family and friends), egocentric (a single-minded attentional focus on the self), and pathological selfishness (inflicting harm upon others for self-advancement purposes).

The Prosocial Tendencies Measure (PTM; Carlo and Randall, 2002, for the model fit of the Serbian adaptation see Dinić and Bodroža, 2020) contains 23 items on a 5-point scale (from 1 = *does not describe me at all* and 5 = *describes me greatly*) that measure six types of prosocial tendencies: altruism (voluntary helping motivated primarily by one's concern for the needs and welfare of others), compliant (helping others in response to a

verbal or non-verbal request), emotional (helping others under emotionally evocative circumstances), dire (helping in crises or emergencies), public (helping in front of an audience, at least partially motivated by the desire to gain the approval and respect of others and enhance one's self-esteem), and anonymous (helping without others being aware of who helped them). Among them, public could be seen as purely egoistic, self-oriented prosocial tendency, altruism as a purely other-oriented tendency, while the rest of them could be sorted out between these extreme categories.

Descriptives and alpha reliabilities are presented in **Table 1**. Reliabilities are consistent to those obtained in the previous studies, including somewhat lower reliability for altruism and dire prosocial tendency, which are low, but still acceptable considering small number of items (e.g., Carlo and Randall, 2002; Carlo et al., 2003; Raine and Uh, 2019). Data and instruments could be found at https://osf.io/gdz42/.

RESULTS

Effects of Demographics on Protective Behaviors

The results showed that compliance with COVID-19 protective behaviors was more frequent among women [$t_{(577)} = -5.25$, $p < 0.001$, $M_{\text{female}} = 3.73$, $SD_{\text{female}} = 0.84$, $M_{\text{male}} = 3.23$, $SD_{\text{male}} = 0.89$], older people, and those who live in households with more people (**Table 1**), but the correlation with educational level was not significant ($\rho = 0.07$, $p = 0.103$). Thus, sex, age, and household size would be added as covariates in further analyses in order to control their effects on explored relations.

Correlations Between Protective Behaviors and Context-Related and Personality Factors

Considering context-related factors, both empathy toward people in forced isolation and fear related to pandemic were positively related to protective behaviors (**Table 1**). Considering personality factors, all prosocial tendencies were positively related to protective behaviors, except for the tendency toward public prosocial behavior, which showed no significant correlation. Mutual correlations between three selfishness subscales were high (0.64, 0.65, and 0.73) and all three scales showed relatively similar intensity of negative relations with protective behaviors (from −0.17 to −0.19, all *p*s < 0.001). Thus, the total score of selfishness was used in further analyses and it showed low negative correlation with protective behaviors (the remaining correlations are reported in **Supplementary Table A**). Therefore, both context-related and individual factors showed significant correlations with protective behaviors. However, it should be noted that all correlations were small.

Prediction of Protective Behaviors

To explore the prediction of protective behaviors based on demographic, context-related, and personality factors, a hierarchical regression analysis was conducted. In the first step, sex, age, and household size were entered to control their effects. In the second step, context related factors (empathy toward people in forced isolation and fear related to the pandemic) were entered. In the third and final step, personality factors (selfishness and prosocial tendencies) were entered. The results showed that both context-related and personality factors significantly contributed to the prediction of compliance with protective behaviors. Personality factors had a significant contribution over and above demographic characteristics and context-related factors (**Table 1**). Among context-related factors, only fear related to the pandemic had a significant positive contribution to compliance with protective behaviors. Although empathy was significant in the second step ($\beta = 0.12$, $p < 0.01$), with the inclusion of personality traits, it became a non-significant predictor. Among personality factors, only selfishness and anonymous prosocial tendency had significant contributions, in opposite directions.

Mediation Effect of Context-Related Factor of Empathy

Mediation effects of empathy toward persons in forced isolation in relations between personality factors and protective behaviors were tested, with sex, age, and household size as covariates in order to control their effects (analyses were conducted in PROCESS macro for SPSS v.3.4, Hayes and Little, 2018). In the mediation analysis, only traits that had a significant contribution to protective behaviors were tested, i.e., selfishness and anonymous prosocial tendency. In the case of selfishness as a predictor, the mediation effect of empathy was significant (**Figure 1A**). Empathy acted as a buffer and weakened the negative effect of selfishness on compliance with protective measures. In the case of anonymous prosociality as a predictor, empathy was also significant mediator and partly explained of the effect of anonymous prosociality on protective behaviors (**Figure 1B**).

MODERATION EFFECT OF CONTEXT-RELATED FACTOR OF FEAR

Moderation analysis showed no significant interaction effect of fear related to pandemic and selfishness ($\Delta R^2 = 0.003$, $p = 0.14$) on protective behaviors, with control of demographic variables. Additionally, there is no significant interaction between fear and anonymous prosocial tendencies ($\Delta R^2 = 0.001$, $p = 0.36$) on protective behaviors.

DISCUSSION

The main result of this study is that both selfishness and prosocial tendencies had effects on protective behaviors over and above demographic and context-related factors, but in opposite directions. Thus, selfishness had negative effects on compliance with protective measures, meaning that more selfish people are less likely to adhere to health-protective measures. Among prosocial tendencies, all but public prosocial tendency showed a significant positive correlation with protective behaviors. However, in the regression analysis, only anonymous prosocial

TABLE 1 | Contributions of demographics, context-related, and personality factors to COVID-19 protective behaviors and correlations.

Variables	β	*r*	*M*	*SD*	α
Control variables: $R^2 = 0.09$* **					
Sex	0.15***	0.16*** (r_{bs})	–	–	–
Age	0.16***	0.16***	34.01	10.27	–
Household size	0.09*	0.09* (ρ)	3.06	1.34	–
Context-related factors: $\Delta R^2 = 0.04$* **					
Empathy toward people in forced isolation	0.03	0.20***	3.91	0.72	0.78
Fear related to the pandemic	0.19***	0.19***	2.78	1.01	0.90
Personality factors: $\Delta R^2 = 0.04$* **					
Selfishness	−0.13**	−0.21***	2.04	0.60	0.90
Dire	0.04	0.09*	3.75	0.78	0.54
Public	0.02	−0.02	1.43	0.60	0.78
Anonymous	0.10*	0.20***	3.29	0.97	0.81
Compliant	0.03	0.15***	4.12	0.80	0.78
Emotional	0.02	0.11**	3.73	0.86	0.77
Altruism	0.02	0.08*	4.29	0.58	0.55
Total $R^2 = 0.17$***					

*Sex was coded as 1 = male and 2 = female; ρ, rho rang correlation; r_{bs}, point-biserial correlation; ***p < 0.001, **p < 0.01, *p < 0.05.*

tendency showed a unique significant contribution. Anonymous prosocial tendency is defined as helping without knowledge of who helped (Carlo and Randall, 2002). In previous studies, it showed no significant correlation with altruism or with Big Five personality traits (e.g., Rodrigues et al., 2017). However, it was positively related to the aspects of both cognitive and affective empathy and global prosocial behavior, while it was negatively related to hedonistic prosocial moral reasoning (Carlo and Randall, 2002; Carlo et al., 2003; Rodrigues et al., 2017). It could be assumed that those who are more other-oriented and prone to anonymous prosocial behavior are less concerned with personal desires and needs and they are characterized by higher emphatic concern, which leads them to practice protective measures. Indeed, a further analysis showed that empathy acts as a mediator in the positive relation between anonymous prosociality and protective behaviors. Additionally, health-irresponsible behaviors among more selfish people could be partially explained by the lack of empathy. This is important from the standpoint of formulating public communication to promote positive behavior change, which should be referred to as protection of the most vulnerable groups and finally, of all others, compared to the protection of oneself (see Jordan et al., 2020).

The results are generally in line with the expectation that prosocial tendencies would be positively related and that antisocial tendencies would be negatively related to compliance with protective measures. However, the non-significant contribution of altruism was not expected. Altruism showed a small positive correlation with protective behaviors, but it was not among the significant unique predictors of these behaviors. Altruism in the PTM refers to helping others when there is little or no perceived potential for a direct, explicit reward to the self (Carlo and Randall, 2002). It is negatively related to approval-oriented prosocial moral reasoning and personal distress and positively related to Agreeableness, but it is

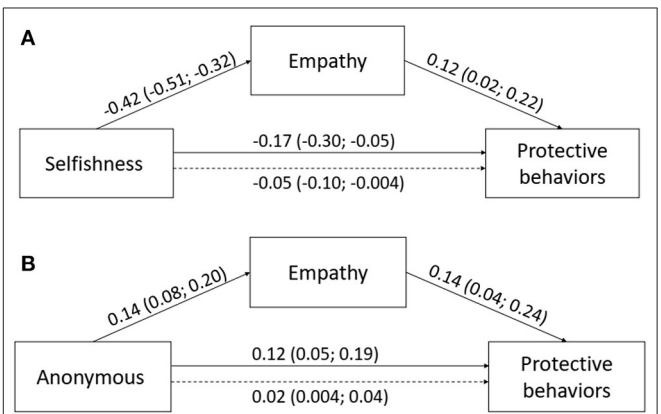

FIGURE 1 | Mediation effect of empathy in relations between selfishness **(A)** and anonymous prosociality **(B)** with protective behaviors. Unstandardized beta coefficients and 95% CIs were presented. Betas below dotted line refers to indirect effects.

unrelated to indicators of empathy and global prosocial behavior (Carlo et al., 2003; Rodrigues et al., 2017). Thus, it seems that global empathic capacity could make the distinction between altruism and anonymous prosocial tendencies. The results support the view according to which the tendency that is linked to empathy obtains the main effect on the practice of protective behaviors (e.g., Pfattheicher et al., 2020). Additionally, in this study, empathy showed a higher correlation with anonymous prosociality ($r = 0.22$) than with altruism ($r = 0.11$, $Z = 1.97$, $p = 0.048$).

In the same vein, one could expect that emotional prosociality had significant effect in predction of protective behaviors. However, emotional prosociality refers to help under emotionally

evocative circumstances, e.g., in the presence of obvious physical pain or distress. Since pandemic do not include such demands as situations that call for fast reacting (as, for example, presence of physical pain), we could assume that this is the reason why emotional component was not a significant predictor of protective behaviors (although it showed significant correlations with it).

Nevertheless, it should be noted that in this study, empathy was measured as a context-related factor, as empathy toward people in forced isolation. In the early stage of the pandemic in Serbia, people in forced isolation included the elderly as the main vulnerable group, but also people who came to Serbia from abroad. Thus, this measure had a narrower scope compared to measures of empathy used in other research (e.g., Pfattheicher et al., 2020).

The results also confirmed the significance of fear related to the pandemic as a positive predictor of protective behaviors, which is in line with previous studies (e.g., Harper et al., 2020). It should be noted that among context-related factors, as opposed to empathy, fear had unique contribution to protective behavior. This result highlights the important role of fear as a strong underlying mechanism of compliance with protective measures. However, fear did not act as a moderator and it seems that, among those with higher selfishness, raising the adaptive fear of pandemic could not change the health-irresponsible behavior.

There are some limitations of the study. First, the sample was convenient, recruited online via social networks. It mostly comprised highly educated participants, which limited the conclusions. Second, the study was limited to the early stage of the COVID-19 pandemic. Cao et al. (2020) showed that empathy and prosocial tendencies decreased in the post-outbreak period. Thus, a different pattern could be expected in longitudinal studies. Third, in the present study, fear was assessed as a general state related to the pandemic. It was not specified whether it referred to fear for oneself or others. Some previous studies showed that fear for relatives was stronger than fear for oneself (e.g., Akdeniz et al., 2020). Therefore, we could expect a different pattern of relations if this was taken into account.

Compared to previous research in which only prosocial (e.g., Blagov, 2020) or only antisocial tendencies (e.g., Nowak et al., 2020) were examined, in this study effects of both types of tendencies were explored since these two tendencies are not simply opposite poles (e.g., Krueger et al., 2001). Results support the view of protective behaviors as forms of prosocial and unselfish behaviors. Furthermore, the antisocial and selfish strategy can decrease the chances of both personal survival and the survival of group members. Finally, one of the novelty contribution of this study is that situational empathy could be seen as the motivational mechanism that could enhance protective behaviors among those who are characterized as more selfish. These findings have practical implications for shaping public messages and they can help effectively promote protective behaviors.

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: Open Science Framework - https://osf.io/gdz42/?view_only=620512fd2ebc484ba53d9a194f58a5a5.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Ethical Committee of the Department of Psychology, Faculty of Philosophy, University of Novi Sad, Serbia, which is the Second Instance Commission of the Ethical Committee of the Serbian Psychological Society (No. 202003221959_nytc). The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

BD and BB contributed to the conception and design of the study, collected the data, and performed the analyses. BD wrote the draft of the manuscript. BB provided substantial feedback on the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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Do Islanders Have a More Reactive Behavioral Immune System? Social Cognitions and Preferred Interpersonal Distances During the COVID-19 Pandemic

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Insular populations have traditionally drawn a lot of attention from epidemiologists as they provide important insights regarding transmission of infectious diseases and propagation of epidemics. There are numerous historical instances where isolated populations showed high morbidity once a new virus entered the population. Building upon that and recent findings that the activation of the behavioral immune system (BIS) depends both upon one's vulnerability and environmental context, we predicted that, during the COVID-19 pandemic, place of residence (island vs. mainland) explains a significant proportion of variance in preferred interpersonal distances, animosity toward strangers, and willingness to punish those who do not adhere to COVID-19 preventive measures. With 48 populated islands, Croatia provides a fruitful testing ground for this prediction. We also opted to explore relations among BIS-related variables (pathogen disgust, germ aversion, and perceived infectability) and social cognitions in a more natural context than has previously been done. The study was conducted online, on Croatian residents, during April and May 2020. As expected, the BIS variables contributed significantly to preferred interpersonal distances, negative emotions toward strangers, and willingness to punish those who do not adhere to COVID-19 preventive measures. Furthermore, our results showed that geographical location explained a significant amount of variance in preferred social (but not personal and intimate) distances and negative emotions toward foreigners. As Croatian islands are extremely frequent travel destinations, these differences between mainlanders and islanders cannot be explained by the lack of exposure to foreigners. Additionally, we found that scores on preferred interpersonal distances, pathogen disgust, and germ aversion were significantly higher compared to those obtained in Croatian samples before the COVID-19 pandemic. Furthermore, men scored higher in perceived infectability than before the COVID-19 pandemic, and women did not, which reflects the objectively higher risk of SARS-CoV-2 for men than for women. Taken together, our results support the notion that BIS is a highly adaptive and context-dependent response system, likely more reactive in more susceptible individuals.

Keywords: behavioral immune system, social cognitions, interpersonal distance, COVID-19, xenophobia

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INTRODUCTION

Epidemics are not a novelty in human evolutionary history. In fact, they have plagued humanity from the very beginnings. Even the recent pandemic caused by the novel coronavirus SARS-CoV-2, leading to deaths of more than 2.7 million people as of March 31, 2021 per the WHO, is not an unprecedented event in human history. Having in mind that humans evolved alongside numerous pathogens, it comes as no surprise that there exists a unique system composed of various cognitive and affective processes and behaviors whose main goal is to protect the organism from coming into contact with the infectious disease in the first place. The behavioral immune system (BIS), as defined by Schaller (2006), has a unique role in shaping a variety of human behaviors, from basic avoidance of rotten food to social cognitions. Disgust, the emotion with a central role in this system, serves as a main motivator toward pathogen and disease avoidance. In other words, the higher the disgust sensitivity or disgust elicited, the higher the motivation to implement stimuli avoiding behaviors (Curtis and Biran, 2001; Oaten et al., 2009).

While BIS activation is closely related to disgust, it also depends on the context and various situational cues that can make disease threats more salient (Schaller, 2016), therefore making behaviors that are a product of BIS activation more pronounced. Indeed, recent findings corroborate the notion that some sort of sensitization to pathogen threat occurred during this global health crisis, resulting in heightened scores on BIS-related traits on a group level (Miłkowska et al., 2021; Stevenson et al., 2021). It should be noted that some authors cautioned against superficial application of BIS theoretical framework in research of psychological processes during a pandemic (Ackerman et al., 2020) and others further elaborated on mismatches between ancestral environments in which the adaptations collectively called BIS may have evolved and contemporary conditions of living (Ackerman et al., 2020; Varella et al., 2021). However, even though sickness cues are not easily detectable in early phases of SARS-CoV-2 infection, especially in asymptomatic cases, contemporary humans collect and process disease-threat relevant information through various channels. The daily updated numbers of new cases and deaths, as well as news about available interventions such as the development of treatment protocols, drugs, and vaccines, are easily accessible on various media platforms; in fact, there is a surplus of information, not a lack thereof, and the resulting *infodemic* has already been associated with a rise in health-related anxiety disorders (Jokic-Begic et al., 2020). In this sense, the COVID-19 pandemic provides a unique opportunity to study BIS in more naturalistic circumstances, as compared to inducing disease salience and pathogen threat artificially via priming.

The last serious outbreak, although much smaller in size than the current one, the Ebola outbreak in 2014, showed that certain social cognitions can become more pronounced during times of disease threat. Kim et al. (2016) showed that, when disease threat is especially salient and when people feel fearful and vulnerable to disease, they also express more xenophobic attitudes. A similar pattern has been observed during this pandemic: people tend to express more negative attitudes toward foreigners (Sorokowski et al., 2020) and increased support for conservative political candidates (Karwowski et al., 2020). In our evolutionary history, outgroup members might have posed a threat because they could have been carriers of some new, previously unencountered pathogen, thus increasing the risk of disease for the in-group. Additionally, outgroup members possibly don't know or understand customs that could have been set in place to minimize the risk of disease spread, thus once again increasing the risk of pathogen transmission for the in-group (Schaller, 2016). Of course, xenophobia directed against group identity markers is unlikely to prevent disease transmission in modern contexts, making group identity only a weak correlate of infection risk (Ackerman et al., 2020). Indeed, it seems that resistance to foreign norms, rather than avoidance of novel pathogens, better explains the relationship between pathogen avoidance and outgroup prejudice (Karinen et al., 2019). However, there is ample evidence that disease and pathogen salience had a role in shaping various cultural specificities (Schaller and Murray, 2010). Cultures that have historically been more exposed to various infectious diseases have more xenophobic and conservative attitudes (Fincher et al., 2008; Murray and Schaller, 2010; Terrizzi et al., 2013). A large cross-cultural study (Tybur et al., 2016) recently showed that national parasite stress relates to traditionalism, defined as an aspect of conservatism especially related to adherence to group norms, but not to social dominance orientation, which is an aspect of conservatism especially related to endorsements of intergroup barriers and negativity toward ethnic and racial outgroups. Schaller and Murray (2008) showed that the association between disease prevalence and regional variability in extraversion, openness to experience and (female) sociosexuality remained significant even after controlling for variety of other variables (e.g., latitude, temperature, life expectancy, and GDP per capita) which might influence these cultural variations.

On the individual level, exposure to a disease prime can lead participants with high perceived vulnerability to disease to rate themselves as less agreeable and less open to experience, facilitate avoidant tendencies (Mortensen et al., 2010), increase ethnocentric attitudes (Navarrete and Fessler, 2006), as well as conformity (Wu and Chang, 2012). Furthermore, sensitivity of the BIS, operationalized through both physiological measures and self-assessments, predicted more negative attitudes toward immigrants (Aarøe et al., 2017). However, xenophobia is not a one-dimensional feature. For example, Faulkner et al. (2004) showed that Canadians had more negative attitudes toward foreigners from subjectively more distant and unknown countries (Mongolia and Peru) than toward subjectively closer and better known ones (Poland and Taiwan), and that participants under high disease-salience conditions expressed less positive attitudes toward foreign, but not familiar, immigrants and were more likely to endorse policies that would favor the immigration of familiar rather than foreign peoples.

Furthermore, it seems that one's own health status mediates BIS (re)activity, i.e., that an organism's physiological needs fine tune BIS activation. For example, recently and frequently ill people showed greater activation of the BIS (Stevenson et al., 2009; Miller and Maner, 2012; Murray et al., 2019), pregnant

women expressed more ethnocentrism in the first trimester, presumably due to immunosuppression (Navarrete et al., 2007; however, the link between progesterone and disgust has been questioned; see Jones et al., 2018), and individuals who possess gene variants associated with greater susceptibility to certain infectious diseases and poorer immunological function reported lower levels of extraversion and openness to experience, as well as higher levels of harm avoidance (MacMurray et al., 2014; Napolioni et al., 2014). These variations in BIS reactivity imply that certain populations might provide valuable deeper insight into the inner workings of the BIS, and isolated populations are certainly among them.

Croatian Island Isolates: The Rationale for This Study

When it comes to infectious disease propagation, living in an isolated area such as an island, is both a "blessing" and a "curse," as it brings both the benefits and dangers of living in isolation. On the one hand, isolation can spare the whole community from being exposed to a pathogen, but on the other hand, this leads to a decreased population immunity, and when a deadly pathogen is re-introduced after a long time, there are no remaining immune individuals (Rudan, 2006). Isolated communities have, throughout history, been hit the hardest when some new infectious disease invades their village or island, leading to numerous deaths (Whittaker, 2018). Their lack of immunity caused by few contacts with the outside world, limited nutrition, household size, drinkable water, and access to sanitation, and healthcare availability among others, all contribute to rapid, and often deadly, spread of disease. It has been suggested that this might have contributed to entire civilizations being wiped out, for instance the inhabitants of the Easter Island and the cultures of Mayas and Aztecs in central America (Rothman and Greenland, 1998). Therefore, it can be speculated that the BIS would be more reactive among isolated populations.

With 48 populated islands, whose populations vary from 1 to 19,383 inhabitants, Croatia provides a fruitful testing ground for this hypothesis, as all other relevant variables which might influence the prophylactic behaviors and related cognitions and emotions, such as the dominant culture, religious beliefs, or the health care system, are equal among islanders and mainlanders. Croatian islands have been inhabited since the time of ancient Greece, and because of their location on important maritime routes, their inhabitants where exposed to various influences, from Rome and Byzantium, the Turkish and Austrian Empires, to the Venetian Republic and France. However, ships did not carry only goods: in addition to the benefits of trade, islanders also experienced numerous epidemics including plague, cholera, leprosy, and malaria and were faced with the need to avoid, prevent, or mitigate epidemics of infectious diseases (Cvetnić, 2014).

Numerous instances of plagues in the Adriatic area have been documented in historical archives, dating from as early as 160 AD. The "black death" ravaging European populations throughout middle ages found its way to Croatian islands by maritime routes (Bačić, 2007). Interestingly, the "black death" outbreak which took a huge toll on the European population in 1348 also brought some important epidemiological insights: it has been noted that outbreaks usually take place after the arrival of ships from distant locations, and thus a mandatory isolation of people and goods from those ships was proscribed. In fact, the world's oldest known quarantine dates back to 1377 in Dubrovnik. The word "quarantine" stems from the word *quarranta*, meaning 40, which is the number of days that travelers arriving to Dubrovnik port had to spend in isolation. Aside from specialized quarantine units called *lazarettos*, some of the smaller Croatian islands in the middle ages were designated as locations for self-isolation and to this day, they bear names like *Gubavac*, meaning leper. There were instances in history when trading between the islands and the mainland was prohibited in order to prevent the spread of a disease. The outbreak in 1617 had the greatest impact on inhabitants of Korčula island: it was brought by sailors on a Venetian ship, spread fast among the local community, eventually eradicating whole lineages of families (Bačić, 2007).

Kralj-Brassard (2016) described the 17th century Dubrovnik Republic as being under constant threat from plague and other contagious diseases coming mostly from the neighboring regions of the Ottoman Empire. However, due to a well-organized system of public health measures against plague, developed and tested for centuries, such as the famous Dubrovnik's *cordon sanitaire*, the number of outbreaks was smaller, their duration shorter, and the scope of contagion limited in comparison with the neighboring regions under Venetian or Ottoman rule. Along with isolating the sick and the travelers, islanders have also been known to self-isolate immediately upon hearing the news of new infections: an interesting example took place in the 19th century on the island of Hvar, where citizens who owned ships self-isolated on their vessels in the city harbor, and stayed there through the entire epidemic of cholera with only scarce food and water supplies, and yet all survived, while the ones who stayed in the city were decimated (Baras, 2020).

Another infectious disease threatening inhabitants of Adriatic islands was malaria. As early as 1420, the Korčula Statute forbade the people of Korčula to sail on the river Neretva, under the threat of punishment of losing all their property. This was a surprisingly appropriate public health measure against malaria—as it legally bound the residents of Korčula to avoid the mosquito-infested Neretva river estuary. Interestingly, Italian travel writer Alberto Fortis wrote in 1774 that he learned from a priest in the Neretva area that malaria is caused by mosquito bites—this was 125 years before Ronald Ross discovered that mosquitos transmit malaria (Eterović, 1994).

Later in history, Croatian islands witnessed surges of cholera, typhus, dysentery, scarlet fever—mostly brought by soldiers coming home from various regions of the Austro-Hungarian empire during WWI. Again, an elaborated set of measures was put in place: special gendarmerie squads patrolling the areas designated for isolation, disinfection protocols, social distance measures, school closures, even mass vaccination campaigns were organized when possible, exemplified by the mandatory vaccination against smallpox on the island of Krk (Kirinčić, 2019.

From the perspective of the BIS theoretical framework, these historical events also bring to light another interesting element, which can be found even in the epidemiological news section of the official *Journal of the Croatian Medical Association* (*Liečnički viestnik*, dating back to 1877) in which overtly xenophobic descriptions are used for certain groups perceived as disease carriers (e.g., "wandering gypsies," "migrant folks," "their folks" vs. "our folks," "dirty ones," etc.).

Given these specific geomorphological, economic, and demographic characteristics, as well as the historical heritage of Croatian islands, their inhabitants certainly represent an interesting study population, and have often been in the focus of geneticists and epidemiologists (see e.g., Rudan et al., 1999; Vitart et al., 2006). As for recent history, an extensive epidemiological study of several infectious diseases (salmonellosis, streptococcal angina, varicella, and scabies) on 10 Croatian islands (Krk, Cres, Lošinj, Rab, Pag, Brač, Hvar, Korčula, Vis, and Lastovo) between 1989 and 1998 showed that in comparison with the Croatian general population, epidemics on islands were less frequent, but of much greater intensity, especially in smaller and very isolated communities (Rudan et al., 2002). Even nowadays, while not isolated in the true meaning of the word, Croatian island towns are still relatively small, often with insufficient healthcare, far away from mainland hospitals, and with modest food supply if further from the coast, especially during off-season (Skračić, 2013).

With lockdown in place during the data collection for this study, islanders were isolated more than ever. Commuting restrictions were put forward, ferries to the mainland were scarce, and health services weren't equipped for an outbreak, making existing disease threat even worse. Even though Croatian islands have long been known as tourist hotspots, and most Croatian islanders financially depend on tourism, during the lockdown of spring 2020, there were anecdotal reports of locals calling the police and reporting seeing "foreigners on the seafront."

Thus, the aim of this study was to explore COVID-19 health anxiety and other BIS-related emotions and cognitions, such as germ aversion, perceived vulnerability to disease, and pathogen disgust in their relation to: (a) negative emotions toward strangers; (b) willingness to punish those who do not adhere to COVID-19 preventive measures; and (c) preferred interpersonal distances. Furthermore, we opted to test the prediction that living in an isolated area contributes significantly to such emotions and cognitions. Additionally, in order to test the possible effect of COVID-19 pandemic on BIS-related emotions and cognitions, we compared the current scores with the ones obtained in similar samples before the pandemic.

MATERIALS AND METHODS

Participants

A total of 805 people, aged 16–71 (M = 35.52, SD = 11.96) participated in the study. Overall, there were 639 female and 166 male participants. Out of the 768 participants who indicated their place of living, there were 412 mainlanders and 356 islanders. Amongst mainlanders, aged 17–67 (M = 34.04, SD = 11.64), there were 326 female and 85 male participants, while amongst islanders, aged 16–71 (M = 37.53, SD = 11.96), there were 284 female, and 69 male participants.

On average, the islanders lived in larger households [F (1, 756) = 7.75; $p < 0.001$], including more young children [F (1, 722) = 22.45; $p < 0.001$], had lower monthly income [F (1, 756) = 88.91; $p < 0.001$], and as expected, their settlements had fewer inhabitants [F (1, 761) = 1063.94; $p < 0.001$]. Participants in our sample estimated their islands to have had an average of 5,900 inhabitants, and the settlement they currently lived in to have had an average of 1,700 inhabitants.

Importantly, islanders in our sample reported having fewer symptoms of respiratory infections in the period preceding the study [F (1, 767) = 28.83; $p < 0.001$], which is an indirect indicator of our assumption that they are indeed less exposed to a whole range of respiratory viruses than the mainlanders.

Pre-pandemic Samples

For the comparison of BIS-related variables before the pandemic with the ones collected for the purposes of this study, we used data from two of our earlier databases (collected online during 2017 and 2019; unpublished data). A total of 957 participants (351 men, 606 women) were comparable to the current sample in age (range 18–88; M = 31.56, SD = 12.56), and economic status (the SES variables were operationalized differently, so a direct statistical comparison is not possible, but the vast majority, approx. 60% of participants in both samples reported having an average income and about 30% reported having an above average income). However, for these samples, we do not have the information whether they lived on an island or on the mainland.

Procedure

The link to the online questionnaire was shared on various social networks, and special attention was given to recruiting islanders through local Facebook groups. The data were gathered during April and May 2020, during the first wave of the COVID-19 pandemic. At that time, the Croatian government implemented a rather restrictive set of measures, restricting travel between counties, outside of special circumstances, social gatherings were restricted to a maximum of 10 people from a maximum of two households, schools went online, grocery shops worked reduced hours, and restaurants, pubs, and cafes were closed, as were all non-essential facilities. In fact, according to the Oxford COVID-19 government response tracker at that time, Croatia ranked as the strictest country on the scale and had the highest stringency index (Hale et al., 2020). Participants read the informed consent and if they agreed to participate, by clicking the "agree" button they were directed to the questionnaire. The first part of the questionnaire consisted of demographic information: gender, age, marital status, education, employment status (if unemployed, they were also asked if they had lost their job since the beginning of the lockdown), household size (including how many children under the age of 12), and household monthly income. They were then asked about their place of living, how many citizens it has, whether it can be considered a tourist hotspot, and if their place of residence is on the mainland or on an island.

If participants were islanders, they were then asked further questions: the size of the population of their island, how the island is connected to the mainland (ferry, catamaran, bridge etc.), how often the connections from island to mainland usually run, and how often they ran during lockdown.

If participants were mainlanders, they were asked whether they lived in a city or in a village. For villagers there were also additional questions: how far away the first bigger town the village is, how often public transport runs between their village and said town, and how often during the pandemic. Originally, we intended to test if there are any differences in BIS-related variables between residents of villages, where the density of population is low, and city dwellers. However, the sample size of people living in rural areas was too small to conduct a meaningful analysis.

The rest of the survey was the same for all participants. First, they were asked several questions concerning coronavirus—whether they, or any of their family members, are at an increased risk of contracting coronavirus and/or developing a complicated clinical presentation of COVID-19 disease, and whether they or anyone they know tested positive for coronavirus. They were also asked if and how has their daily life changed since the beginning of the pandemic. In addition, participants were asked to check the symptoms they have experienced during the last three weeks (if any). The symptoms listed were: stuffed nose, sneezing, sore throat, coughing, runny nose, headache, shivering, weakness/nausea. Afterward, they were asked to fill out various questionnaires to assess their COVID-19 anxiety, inclination toward punishing those who do not adhere to preventive COVID-19 measures, perceived vulnerability to disease, emotions toward strangers, conservatism, preferred interpersonal distances, and pathogen disgust proneness.

Materials

COVID-19 Anxiety Scale

As a measure of COVID-19 anxiety, we used a COVID-19 concerns scale (Lauri Korajlija and Jokić-Begić, 2020). The scale consists of 5 items depicting various concerns regarding the impact of coronavirus on health including perceived likelihood of infection, perceived danger of COVID-19, and others. Participants had to indicate the extent to which an item relates to them on a scale ranging from 1 (not at all) to 5 (very much). The scale has good reliability (Cronbach $\alpha = 0.78$).

Perceived Vulnerability to Disease

Perceived vulnerability to disease was measured using the scale developed by Duncan et al. (2009). This scale has 15 items that constitute two subscales: the Perceived infectability subscale (7 items) and Germ aversion subscale (8 items). Participants have to indicate their agreement with the items on a 1 (Strongly disagree) to 7 (Strongly agree) scale. The scale had very good overall reliability (Cronbach $\alpha = 0.82$). The same was true for perceived vulnerability to disease subscale ($\alpha = 0.87$), while germ aversion had good reliability ($\alpha = 0.74$).

Disgust

Disgust proneness was measured using The Pathogen subscale of the Three Domains of Disgust Scale developed by Tybur et al. (2009). It has three subscales: pathogen disgust, moral disgust, and sexual disgust, but in this study only the pathogen disgust subscale was used. The subscale has 7 items describing situations that are considered disgusting, as they signal pathogen threat, and participants have to rate the items on a scale of 0 (not at all disgusting) to 6 (extremely disgusting) with three being a neutral value. The subscale had good reliability in this study ($\alpha = 0.74$).

Conservatism

Social conservatism subscale of the 12-item Social and Economic Conservatism Scale (SECS) (Everett, 2013) was used to measure participants' conservatism. The subscale consists of 7 items (abortion, army and national security, religion, traditional marriage, traditional values, family, and patriotism) and participants were asked how they feel about each item on a scale of 0–100, with 0 meaning "very negative", 100 meaning "very positive" and 50 meaning "not negative nor positive". The subscale yielded very good reliability, $\alpha = 0.801$. The economic conservatism subscale was omitted, as it has previously been shown that this construct is not comparable between Croatian and United States samples (thus, the validity of this subscale for use in Croatian samples is debatable; Mrakovčić and Buršić, 2017).

Preferred Interpersonal Distances

To measure preferred interpersonal distances, we used a graphic task developed by Sorokowska et al. (2017). This instrument measures three different preferred interpersonal distances—preferred distance to a stranger (social distance), an acquaintance (personal distance), and a close person (intimate distance). Participants are presented with two human figures, one on each end of the scale, labeled A and B. They were instructed to imagine that they were person A and to rate how close the person B could approach them, in order for them to still feel comfortable. The distance on the scale ranged from 0 to 220 cm, and each participant gave three assessments: if the person B was a stranger, an acquaintance, or a close person. Before the COVID-19 pandemic, on a sample size of 614 participants, the values obtained in Croatia for preferred interpersonal distances were: $M = 108.86$ (SD = 28.74) for strangers, $M = 89.61$ (SD = 24.06) for acquaintances, and $M = 76.16$ (SD = 23.84) for close persons (Sorokowska et al., 2017).

Negative Intergroup Emotions Scale

This scale was developed by Stephan et al. (1999) and is used as a measure of affective component of attitude. It consists of six positive and six negative emotions and participants have to indicate the extent to which they feel a certain emotion toward strangers on a 1 (not at all) to 7 (very much) scale. Before calculating the final score, positive emotions need to be recoded so that the higher result indicates more negative emotions. In this study, the scale had a good reliability of $\alpha = 0.77$.

Inclination to Punish Non-adherence to COVID-19 Preventive Measures

Participants were presented with two statements about their inclination toward punishing those not abiding by the rules set by the government ("I want the government to harshly punish everyone who is breaking the rules and is not staying at home" and "It is essential for the government to punish people who don't respect the rules of social distancing") and they had to indicate their agreement with the statements on a scale from 1 ("Strongly disagree") to 5 ("Strongly agree").

RESULTS

The data was analyzed using SPSS Statistics for Windows, Version 26.0 (IBM Corp, 2019 Released 2019) and JAMOVI (The jamovi project, 2021).

Predictors of Negative Emotions Toward Foreigners

A two-stage hierarchical multiple regression analysis was conducted with demographic variables (including the geographical location: island vs. mainland) entered at stage one. Here we included conservatism, to control for the fact that islanders tend to be more conservative than mainlanders [Državno izborno povjerenstvo republike Hrvatske (DIP), 2020]. The BIS-related variables entered at stage two included: the perceived infectability and the germ aversion subscales of the Perceived vulnerability to disease scale, the pathogen disgust subscale of the Three domain disgust scale.

As can be seen from **Table 1**, the hierarchical multiple regression revealed that variables entered at stage one contributed significantly to the regression model, [F (5, 512) = 5.84, $p < 0.001$] and accounted for 5.4% of the variation in negative emotions toward foreigners. The only single significant variable contributing to this was the geographical location (islands vs. mainland). Introducing the BIS variables explained an additional 4.5% of variation in the dependent variable and this change in R^2 was significant, F (8, 509) = 6.98, $p < 0.001$. When all eight independent variables were included in stage two of the regression model, the most important predictor of negative emotions toward foreigners was pathogen disgust, followed by perceived infectability, geographical location, age, and gender.

TABLE 1 | Summary of hierarchical regression analysis for variables predicting negative emotions toward foreigners.

Variable	B	*t*	*sr*	*R*	R^2	ΔR^2
Step 1						
Gender	−0.080	−1.867	−0.080	0.232	0.054	0.054
Age	−0.078	−1.808	−0.077			
Settlement population size	−0.039	−0.630	−0.027			
Geographical location	0.181	2.683**	0.115			
Conservatism	0.020	0.46	0.200			
Step 2						
Gender	−0.107	−2.150*	−0.091	0.314	0.099	0.045
Age	−0.088	−2.171*	−0.092			
Settlement population size	−0.053	−0.931	−0.039			
Geographical location	0.168	2.544*	0.107			
Conservatism	0.002	0.041	0.002			
Germ aversion	0.021	0.418	0.018			
Perceived infectability	0.122	2.82*	0.119			
Pathogen disgust	0.167	3.49***	0.147			

$^{***}p < 0.001$. $^{**}p < 0.01$. $^{*}p < 0.05$.

Predictors of Inclination to Punish Those Who Do Not Adhere to COVID-19 Preventive Measures

A two-stage hierarchical multiple regression analysis was conducted with demographic variables entered at stage one. Here we also included conservatism, to control for the fact that islanders tend to be more conservative than mainlanders. The BIS-related variables entered at stage two included: the perceived infectability and the germ aversion subscales of the Perceived vulnerability to disease scale, the pathogen disgust subscale of the Three domain disgust scale, and the COVID-19 anxiety scale.

As can be seen from **Table 2**, the hierarchical multiple regression revealed that variables entered at stage one contributed significantly to the regression model, [F (5, 512) = 14.89, $p < 0.001$] and accounted for about 10% of the variation in willingness to punish rule-breakers. Conservatism had a significant impact here, explaining 6.4% of variance in the dependent variable. Introducing the BIS variables explained an additional 18% of variation in the dependent variable and this change in R^2 was significant, F (9, 508) = 21.71, $p < 0.001$. When all eight independent variables were included in stage two of the regression model, the most important predictor of willingness to punish those who do not adhere to the preventive measures was COVID-19 anxiety which uniquely explained

TABLE 2 | Summary of hierarchical regression analysis for variables predicting inclination to punish those who do not adhere to COVID-19 preventive measures.

Variable	β	*t*	*sr*	*R*	R^2	ΔR^2
Step 1						
Gender	0.162	3.86***	0.162	0.314	0.099	0.099
Age	0.007	0.17	0.007			
Settlement population size	−0.062	−0.92	−0.039			
Geographical location	−0.076	−1.14	−0.048			
Conservatism	0.260	6.02***	0.252			
Step 2						
Gender	0.105	2.76**	0.104	0.527	0.278	0.179
Age	−0.069	−1.78	−0.067			
Settlement population size	−0.096	−1.59	−0.060			
Geographical location	−0.070	−1.17	−0.044			
Conservatism	0.182	4.54***	0.171			
Germ aversion	0.183	4.08***	0.154			
Perceived infectability	0.019	0.48	0.018			
Pathogen disgust	0.063	1.47	0.055			
COVID-19 anxiety	0.319	7.59***	0.286			

$^{***}p < 0.001$. $^{**}p < 0.01$.

8.2% of the variation in the dependent variable, followed by conservatism and gender.

Predictors of Preferred Interpersonal Distances

Three two-stage hierarchical multiple regression analyses were conducted with demographic variables (including the geographical location: island vs. mainland) entered at stage one, and the BIS-related variables (the perceived infectability and the germ aversion subscales of the Perceived vulnerability to disease scale, the pathogen disgust subscale of the Three domain disgust scale, and COVID-19 anxiety scale) were entered at stage two. The dependent variables were preferred interpersonal distances: social distance (stranger), personal distance (acquaintance), and intimate distance (close person). The results can be seen in **Table 3**.

Social Distance (Stranger)

As can be seen from **Table 3** (first column), the hierarchical multiple regression revealed that variables entered at stage one contributed significantly to the regression model [F (5, 511) = 3.38, $p < 0.01$] and accounted for 3.2% of the variation in preferred social distance. Single variables with significant contribution at this step were age, household size, and geographical location. Introducing the BIS variables explained an additional 12% of variation in preferred social distance and this change in R^2 was significant, F (9, 507) = 10.09, $p < 0.001$. When all nine independent variables were included in stage two of the regression model, the most important predictors of preferred social distance were germ aversion and COVID-19 anxiety scale, followed by household size and geographical location.

Personal Distance (Acquaintance)

As can be seen from **Table 3** (second column) the hierarchical multiple regression revealed that variables entered at stage one contributed significantly to the regression model, F (5, 511) = 3.41, $p < 0.01$, and accounted for 3.2% of the variation in preferred personal distance. Age was the only variable with significant contribution at this step. Introducing the BIS variables explained an additional 12% of variation in preferred social distance and this change in R^2 was significant, F (9, 507) = 10.09, $p < 0.001$. When all nine independent variables were included in stage two of the regression model, the most important predictors of preferred social distance were COVID-19 anxiety (accounting for 4.3% of total variance) and germ aversion (accounting for almost 3% of total variance), followed by age.

Intimate Distance (Close Person)

As can be seen from **Table 3** (third column), the hierarchical multiple regression revealed that variables entered at stage one did not contribute significantly to the regression model, F (5, 486) = 1.85, $p = 0.10$. Introducing the BIS variables explained an additional 7% of variation in preferred intimate distance which yielded a significant change in R^2, F (9, 482) = 5.01, $p < 0.001$. When all nine independent variables were included in stage two of the regression model, the only important predictors of preferred intimate distance were COVID-19 anxiety and germ aversion. It is interesting to note though that germ aversion and COVID-19 anxiety were the only two predictors with significant contributions to the preference for all three interpersonal distances.

To check for possibility that geographical location serves as a moderator between the BIS-related variables and criterion variables, we re-ran all the analyses (using *medmod* module in JAMOVI), adding interactions between BIS-variables and geographical location (island vs. mainland). Out of 15 possible interactions (three BIS-related variables combined with five criterions: negative emotions toward foreigners, willingness to punish non-adherence, and three types of interpersonal differences), only two proved significant: geographical location moderated only the relationship between germ aversion and negative emotions toward strangers ($b = 0.234$, $p = 0.027$) and between pathogen disgust and negative emotions toward strangers ($b = 7.56$, $p = 0.025$) with those associations in both cases being more pronounced among islanders than mainlanders.

Since preferred interpersonal distances have previously been shown to depend not only upon culture, but gender and context as well (see Vranić, 2003; Iachini et al., 2016; Sorokowska et al., 2017), we opted to explore them in more detail. In order to do so, we conducted a repeated measures MANOVA with gender (men/women) and geographical location (mainland/island) as between-subjects source of variance and type of interpersonal distance (social/personal/intimate distance) as a within-subject source of variance. There was a significant main effect of gender, with women overall preferring larger interpersonal distances [F (1, 643) = 5.51; $p < 0.02$]. With regard to geographical location (mainland/island), there was no significant main effect on preferred interpersonal distances [F (1, 647) = 2.11; $p = 0.14$]. However, there was a significant interaction between geographical location and type of interpersonal distance [F (1, 647) = 3.12; $p = 0.04$], stemming from the fact that islanders preferred larger social distances than mainlanders, but there were no differences in preferred personal and intimate distances. Furthermore, as expected, there was a significant within-subjects effect, with the preferred social distances being the largest, followed by personal distances and intimate distances were the smallest [F (1, 647) = 415.37; $p < 0.001$]. This can be seen in **Figure 1**.

Is There a Difference in BIS-Related Variables From Before COVID-19?

To answer this question, we compared these scores with the ones obtained before the COVID-19 pandemic. The data for interpersonal distances were collected as a part of large cross-cultural study (see Sorokowska et al., 2017) and the data for germ aversion, perceived infectability, and pathogen disgust scales were collected online during 2017 and 2019 (Hromatko, unpublished data). As can be seen from **Tables 4**, **5**, scores on relevant variables (germ aversion, perceived infectability, pathogen disgust, and preferred interpersonal differences) were significantly higher in this sample, as compared to our pre-pandemic samples. As expected, women expressed significantly higher levels of pathogen disgust, germ aversion, and perceived

TABLE 3 | Summary of hierarchical regression analyses for variables predicting preferred interpersonal differences.

Dependent variable	**Social distance (stranger)**					**Personal distance (acquaintance)**					**Intimate distance (close person)**				
Predictors:	β	*t*	*sr*	R^2	ΔR^2	β	*t*	*sr*	R^2	ΔR^2	β	*t*	*sr*	R^2	ΔR^2
Step 1															
Gender	0.030	0.68	0.030	0.032	0.032	0.071	1.64	0.071	0.032	0.032	0.112	2.49*	0.112	0.019	0.019
Age	0.105	2.36**	0.103			0.167	3.77***	0.164			0.045	0.99	0.044		
Settlement population size	0.067	0.96	0.042			0.016	0.23	0.010			−0.054	−0.77	−0.034		
Household size	0.103	2.29**	0.100			0.021	0.46	0.020			−0.016	−0.34	−0.015		
Geographical location	0.129	1.88*	0.082			−0.009	−0.13	−0.006			−0.004	−0.05	−0.002		
Step 2															
Gender	−0.009	−0.22	−0.009	0.152	0.120	0.032	0.77	0.032	0.152	0.12	0.080	1.82	0.079	0.085	0.067
Age	0.049	1.15	0.047			0.105	2.48*	0.102			−0.002	−0.035	−0.002		
Settlement population size	0.047	0.72	0.029			−0.004	−0.06	−0.002			−0.065	−0.95	−0.041		
Household size	0.094	2.21*	0.090			0.015	0.35	0.014			−0.021	−0.47	−0.021		
Geographical location	0.128	1.97*	0.081			−0.007	−0.12	−0.005			−0.008	−0.11	−0.005		
Germ aversion	0.222	4.85***	0.198			0.193	4.20***	0.172			0.121	2.52*	0.110		
Perceived infectability	0.048	1.11	0.045			0.022	0.51	0.021			0.022	0.47	0.021		
Pathogen disgust	0.029	0.65	0.027			0.018	0.39	0.016			0.067	1.42	0.062		
COVID-19 anxiety scale	0.186	4.09***	0.167			0.231	5.08***	0.208			0.171	3.57**	0.155		

$^{***}p < 0.001$. $^{**}p < 0.01$. $^{*}p < 0.05$.

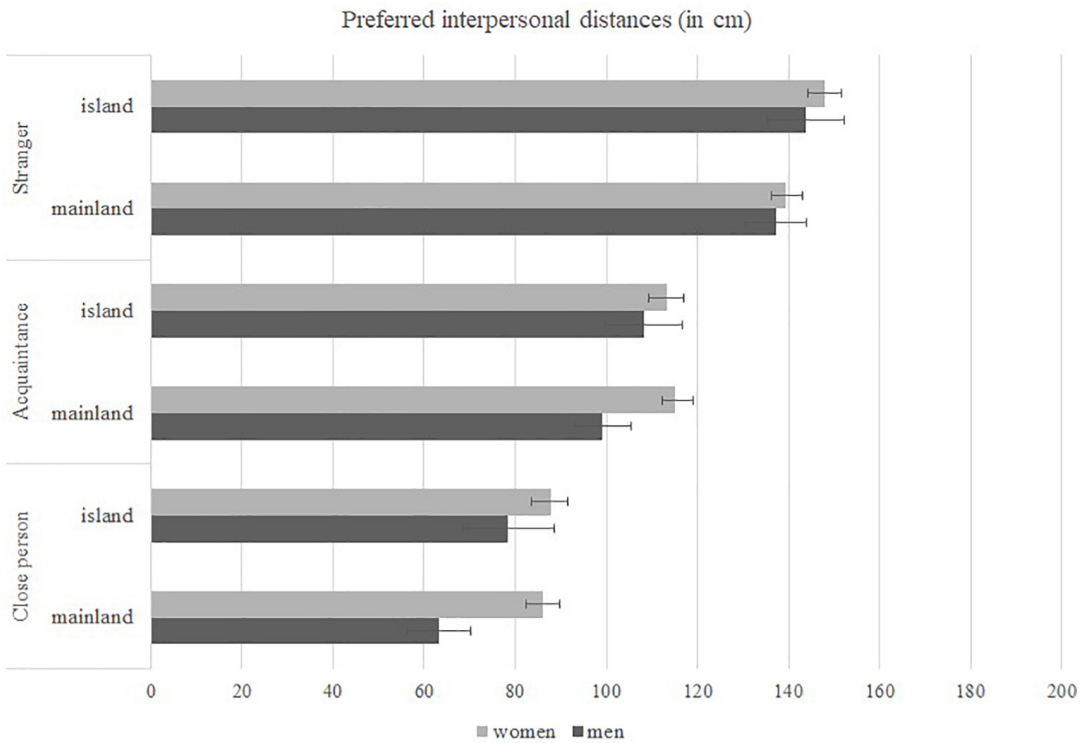

FIGURE 1 | Preferred interpersonal distances (in cm) as a function of geographical location (island vs. mainland) and gender.

infectability than men, and there was only one significant gender × time interaction: only men showed an increase in perceived infectability during the pandemic. Additionally, to control for the possibility that the shifts from pre-pandemic to pandemic scores were driven by the larger proportion of women in our samples, we conducted separate analyses for men and women. The effect remained robust for men, as they had significantly higher pandemic than pre-pandemic scores in pathogen disgust ($F = 4.06$, $p = 0.04$), germ aversion ($F = 35.48$, $p < 0.001$), and infectability ($F = 7.51$, $p = 0.01$). Women had significantly higher pandemic than pre-pandemic scores in pathogen disgust ($F = 10.19$, $p < 0.001$), and germ aversion ($F = 113.87$, $p < 0.01$), with no change in perceived infectability ($F = 0.02$, $p = 0.88$). Considering that we did not have information about the geographical location (island vs. mainland) of the participants in our pre-pandemic samples, but it is reasonable to assume that those were mostly mainlanders, we re-ran the same analyses without islanders in the pandemic sample, and the results remained the same. This was expected, as there were no overall differences in BIS-related variables between mainlanders and islanders ($F_{pathogen.disgust} = 0.06$, $p = 0.80$; $F_{germ.aversion} = 1.75$, $p = 0.19$; $F_{infectability} = 2.14$, $p = 0.14$).

DISCUSSION

The main aim of this study was to determine whether certain social cognitions, namely negative emotions toward strangers, inclination to punish rule breakers (those who do not adhere to COVID-19 preventive measures), and preferred interpersonal distances can at least partly be explained as a result of BIS activation. Furthermore, we opted to gather some insights into the workings of this system in semi-isolated populations of islanders. As we have already stated, we cannot claim that the population of Croatian islanders nowadays is isolated in a classical anthropological sense. However, they do retain some aspects of a more traditional lifestyle, with larger family units within smaller communities and limited connections with the mainland, depending on the island, the frequency of marine lines varies between several lines daily to several weekly, which does make them a semi-isolated population. Furthermore, Croatian island populations were recognized as one of the best-characterized isolate resources in Europe, and as such are included in the "European Special Population Research Network," a project funded by the European Commission and aimed at studying the determinants of human health and disease (Rudan, 2006).

There are also advantages to the fact that the islanders in our sample share a lot in common with the country's mainlanders, as this makes the two groups more comparable, and we can make more specific claims regarding our findings. Local folklore and variations in norms and customs notwithstanding, these participants do share a common culture with their mainland compatriots in the form of sharing the same language, religious views, and political system among others, meaning that alternative explanations of our findings are less likely.

TABLE 4 | BIS-related measures before/during the COVID-19 pandemic.

	Pathogen disgust		Germ aversion		Infectability	
	Men	Women	Men	Women	Men	Women
	M (SD)	*M* (SD)	*M* (SD)	*M* (SD)	*M* (SD)	*M* (SD)
Before pandemic	3.438 (1.185)	3.966 (0.992)	3.577 (1.077)	3.800 (1.027)	2.782 (1.115)	3.189 (1.342)
During pandemic	3.763 (2.201)	4.109 (1.086)	4.216 (1.028)	4.459 (1.073)	3.079 (0.976)	3.199 (1.098)
ANOVA	***F* (1, 1597)**	**Partial η^2**	***F* (1, 1640)**	**Partial η^2**	***F* (1, 1642)**	**Partial η^2**
Time (pre-pandemic/pandemic)	10.616***	0.007	111.26***	0.064	4.939*	0.003
Gender (men/women)	36.779***	0.023	14.301***	0.009	14.483***	0.009
Time × gender	1.591	0.001	0.025	0.000	4.286*	0.003

$^{***}p < 0.001$. $^{**}p < 0.01$. $^{*}p < 0.05$.

TABLE 5 | Preferred physical distances before/during the COVID-19 pandemic.

	Before the pandemic (2016; *N* = 614)		During the pandemic (2020; *N* = 684)		
	M	SD	*M*	SD	*t*
Stranger (social distance)	108.86	28.74	142.10	55.7	13.29***
Acquaintance (personal distance)	89.61	24.06	112.17	55.24	9.32***
Close person (intimate distance)	76.16	23.84	83.45	62.97	2.69**

$^{***}p < 0.001$; $^{**}p < 0.01$.

For example, we can exclude different religious practices as an intervening variable mediating the relation between perceived vulnerability to disease or pathogen disgust and preferred social distance.

Islanders in our sample reported having significantly fewer symptoms of respiratory illnesses in the period preceding the study, which we believe is an important indicator of their reduced exposure to various "common-cold" causing viruses. This was important for our hypothesis, because, as we have elaborated earlier, isolated populations are shielded from exposure to various pathogens, but that also makes them more vulnerable once a new pathogen finds its way to the population. Pathogens are more likely to spread faster, partly because of this lack of previous exposure and subsequent lack of population immunity, and partly because of the way of life. Islanders live in larger, multigenerational households and they are more likely to gather at the same "hotspots" in their local communities, seeing as there is often only one post-office, one grocery shop or market, one church, one general practitioner, or family practice, covering medical needs of all generations, which facilitates the spread of a contagious disease. Thus, the finding that islanders experienced less respiratory symptoms in the period preceding the COVID-19 pandemic than the mainlanders does not imply they have greater biological predisposition to fight off infection; rather it indicates that they were indeed shielded from a variety of other, common respiratory viruses. City dwellers are more exposed to them, as they cannot avoid crowded, closed spaces, such as public transportation or large office buildings with inappropriate ventilation systems. Recent studies have suggested that earlier exposure to other human coronaviruses (often called common cold coronaviruses) makes one if not immune, then at least less likely to develop a complicated clinical presentation of COVID-19 (Guthmiller and Wilson, 2020; Mateus et al., 2020; Sagar et al., 2021). Another non-biological reason why islanders might be at greater risk if they contract the infection is that it will take them longer to get medical help, since they need to reach the mainland, either by marine routes or, in cases of extreme emergency, by air. This was the basis for our prediction that islanders should show greater BIS reactivity.

Negative Emotions Toward Foreigners

As stated earlier, xenophobia might be at least partially explained as a consequence of disease avoidance, and similar patterns of xenophobic escalations have been reported in previous epidemics, as well as this one (Sorokowski et al., 2020). Our analyses (see **Table 1**) showed that, after controlling for conservatism, the only significant variable contributing to negative emotions toward foreigners in the first step of the analysis was place of residence: living on an island correlated significantly with higher animosity toward strangers. This predictor remained significant even after the introduction of a set of variables pertaining to the BIS, when the most important single predictor of negative emotions toward foreigners became pathogen disgust, followed by perceived infectability. As expected, participants with higher scores on BIS variables expressed more negative emotions toward foreigners. Women and older participants expressed fewer negative emotions toward foreigners.

As far as avoidance mechanisms are concerned, these findings are in line with the notion that, especially during the pandemic, when cues of risk of infection are abundant, xenophobic attitudes might serve as a steering wheel, keeping one from coming into close contact with a possible disease carrier. Our prediction that this shall be more pronounced among islanders, was confirmed. As we have argued in the introduction, we do not believe that this difference would be easily attributed to islanders' lack of experience with foreigners, as most of them in one way or another depend upon tourism, and during the summer Croatian islands become tourist hotspots. Even though contemporary humans live in a global world, exposed to various cultures and as some have

argued (e.g., Ackerman et al., 2020) would have no use of applying the same small-scale society heuristics of foreigners being the potential carriers of new pathogen, we have witnessed that in the context of a global health crisis such as this one, it does not take much for a (re)activation of a sort of "mental *cordon sanitaire*." The fact that scores on disgust sensitivity, germ aversion, and perceived infectability have risen significantly in comparison to pre-pandemic scores (Miłkowska et al., 2021; Stevenson et al., 2021) is in line with this notion. The distinction between the proactive and reactive aspects of outputs generated by the BIS (Ackerman et al., 2018) might be of special importance here, as there is no doubt that in this particular scenario, we are dealing with reactive responses. These responses are induced by the presence of information connoting an immediate infection risk, and even if the pathogen threat cannot be detected through our own sensory routes, due to a lack of obvious signs of infection, the awareness of the risk is still heightened.

As our study was conducted during a lockdown, accompanied by a rather strict set of measures, islanders were shielded within their small communities and likely felt threatened by the possibility of outsiders carrying the disease into their, at that time, rather closed communities. Mainlanders, especially those living in larger cities, still used public transport and continued interacting with strangers on a daily basis, often in crowded spaces, and thus may have been desensitized to such situations. Triggers for the BIS activation would have remained the same, but the intensity of their responses could have been attenuated, due to repeated exposure to situations in which contagion is possible. To illustrate this dynamic in a more anecdotal way, in March 2020 the capital of Croatia, Zagreb, was hit by the strongest earthquake since 1880, followed by numerous aftershocks (see e.g., Markušić et al., 2020), leaving over 1,900 buildings uninhabitable by the earthquake damage. Numerous citizens of the capital then tried to find refuge at the coastal parts of Croatia, which led to a public outcry by the locals worried that this will enable the propagation of COVID-19 contagion. Police had to intervene and prevent people from leaving the capital (HINA, 2020; Raić Knežević, 2020).

Inclination to Punish Those Who Do Not Adhere to COVID-19 Preventive Measures

Humans have an evolved tendency to punish social-norm breakers (Krebs, 2008). For an interesting discussion about non-compliance with safety measures as a free-riding strategy and psychological mechanisms aimed at curbing free riding in context of COVID-19 pandemic, see Yong and Choy (2021). We predicted this tendency to punish non-adherence to preventive guidelines would be even more pronounced in situations such as this, where breaking certain rules designed to prevent the spread of a disease directly puts other members of the group in danger. Our results (**Table 2**) showed that conservatism and gender had a significant impact here, explaining 10% of variance in the dependent variable: conservatives and women were more likely to agree with the statements that government should punish severely those who do not adhere to COVID-19 preventive measures. Introducing the BIS variables explained additional 18% of variation in the dependent variable, and the most important predictor of willingness to punish those who do not adhere to the preventive measures was COVID-19 anxiety which uniquely explained 8.2% of the variation in the dependent variable, followed by germ aversion, conservatism, and gender. Expectedly, BIS variables were positively correlated with the dependent variable.

It should be noted that, unlike in some United States samples (see e.g., Calvillo et al., 2020; Corpuz et al., 2020), in our sample social conservatism correlated positively with the inclination to punish those who do not adhere to COVID-19 preventative measures. We expected a positive association, as the social component of conservatism aligns with traditionalism or the endorsement of traditional values, such as family, patriotism, loyalty, and norm-following. Also, the finding that conservatism differentially predicts COVID-19 preventative measures adherence in United States and Croatian samples is in line with the finding that this particular scale (Everett, 2013) has a different factorial structure in Croatian and United States samples (Mrakovčić and Buršić, 2017). As Calvillo et al. (2020) have suggested, the relationship between political ideology and threat perceptions may depend on issue framing by political leadership and media. Furthermore, when it comes to endorsement of authoritarian policies intended to mitigate the effects of the COVID-19, authoritarianism might be a more suitable psychological correlate than conservatism (Manson, 2020).

As for women, their higher inclination for punishment of those who do not adhere to COVID-19 preventive measures might be a result of their traditional role of homemakers: women are more likely to tend to children, sick, and elderly, and in this case, they are the ones who risk more by contracting the virus and potentially transmitting it to their families. For an in-depth review of these sex differences and their impact on pandemic leadership, pertaining to the fact that female leaders seem to be more focused on minimizing direct human suffering caused by the SARS-CoV-2 virus, while male leaders implement riskier short-term decisions, possibly aiming to minimize economic disruptions, see Luoto and Varella (2021). Furthermore, when making moral judgments, women are more likely to take into account the consequences of one's actions, alongside the moral norms (Rothbart et al., 1986). Women on average, tend to be more anxious, and this was the case in our sample as well, with women having higher scores in COVID-19 anxiety. It has been shown earlier that people prefer less risk when the threat of illness was high (Prokosch et al., 2019). All these could have contributed to women's higher inclination to punish those who do not behave responsibly, and those whose actions they might have perceived as being potentially harmful for their families.

Regarding this dependent variable, we didn't find any differences between islanders and mainlanders. However, we are not convinced that this implies that there are no differences in BIS reactivity between these two populations. It is more likely that the measure itself was not elaborated enough to catch the subtle, non-formal ways of detecting and punishing social rule breakers. This

was an *ad hoc* two-item measure, and both items pertained to the government's role in implementing the punishment. In fact, a more nuanced scale, assessing one's willingness to engage in non-formal ways of governing the behavior of others and streaming them into predefined modes of expected and acceptable behaviors would be a better choice, especially in the context of previous research showing that various dimensions of conservatism have different relations to parasite stress (Tybur et al., 2016). However, we were motivated to keep our questionnaire as short as possible in order to keep participants motivated.

Preferred Interpersonal Distances

Since many diseases can spread by a simple touch (Schweon et al., 2013), and with our recent experience with a highly virulent aerosol-borne pathogen, it should not come as a surprise that increasing interpersonal distance has historically been an important aspect of behavioral adaptation against epidemics (Fenichel, 2013), and that similar adaptations have been observed among other species (Goodall, 1986; Schaller, 2011). It has even been suggested that cross-cultural differences in preferred interpersonal distances can be explained by parasite stress (see e.g., Sorokowska et al., 2017).

This was the rationale for choosing our final set of criteria: social, personal, and intimate distances. Here, we expected the largest effects of the BIS activation to be seen in preferred social distance, meaning the distance between oneself and a stranger. We expected smaller effects to be seen for preferred personal distance, meaning the distance between oneself and an acquaintance, and the smallest effects for the preferred intimate distance, meaning the distance between oneself and someone who is close to us.

As can be seen in **Table 3**, our predictors explained up to 15.2% of the variance in preferred interpersonal distances, leaving quite a large proportion of variance unexplained. However, it should also be noted that the variance in these dependent variables was greatly reduced due to the fact that there is an epidemic and that we have been instructed over and over again to keep a distance of minimum 2m. For example, for a stranger, 13.5% of our participants put the slider at the very end of scale (220 cm), which clearly indicates that the variability of true responses was artificially reduced with this scale. However, we wanted to be able to compare the results to the ones obtained before the pandemic, so we kept the original graphic scale (Sorokowska et al., 2017). Even with this limitation, we found a significant contribution of geographical location, with islanders preferring larger social distances. Household size and age were also significant, both positive, meaning that older people and those living in larger households preferred larger distances. This makes sense considering that in the case of COVID-19 age is one of the major risk factors for developing a severe form of illness. Furthermore, people living in larger households are more likely to have an older member of the family, or an immunocompromised one, or a small child in their care living with them, and are more motivated to reduce the risk of contagion. Furthermore, even though islanders in our sample lived in larger households, the contribution of living on an island was still a significant independent predictor of preference for larger social distance. Introducing the BIS variables explained an additional 12% of variation in preferred social distance. When all nine independent variables were included in stage two of the regression model, the most important predictors of preferred social distance were COVID-19 anxiety scale, followed by germ aversion, household size, and finally geographical location.

As for personal distances, the regression model revealed that in the first step age was the only variable with significant contribution. Again, older people preferred larger personal distances. The BIS variables explained an additional 12% of variance, with the most important predictors being COVID-19 anxiety (accounting for 4.3% of total variance) and germ aversion (accounting for almost 3% of total variance), followed by age. All these findings are in line with the idea that perceived risk of contracting a disease, along with parameters, such as age, which objectively put one in a riskier position, shall be associated with preference for keeping a safe distance. There was no significant contribution of the geographical location, which is not surprising, given the fact that on most islands almost everyone is at least an acquaintance, and their whereabouts during the lockdown were well-known which means that they do not pose such a contagion threat as potentially disease-carrying strangers. The same holds true for intimate distance. Here, the whole set of demographic variables failed to explain a significant proportion of the variance in the dependent variable, although gender as a single predictor was significantly correlated with women preferring larger intimate distances. Introducing the BIS variables explained an additional 7% of variance and when all nine independent variables were included in stage two of the regression model, the only important predictors of preferred intimate distance were COVID-19 anxiety and germ aversion. It is interesting to note that germ aversion and COVID-19 anxiety were the only two predictors with significant contributions to the preference for all three interpersonal distances, indicating that, even in interactions with familiar and close persons, the reactivity of the BIS still moderates the preferred physical distance.

Since there were some conflicting results in earlier literature regarding gender differences in preferred interpersonal distances (see e.g., Sorokowska et al., 2017 in comparison with Ozdemir, 2008 or Vranić, 2003), we opted to explore gender differences and their possible interaction with geographical location in greater detail. To that aim we conducted a repeated measures MANOVA with gender (men/women) and geographical location (mainland/island) as a between-subjects source of variance and type of interpersonal distance (social/personal/intimate distance) as a within-subject source of variance. We found a significant main effect of gender, with women preferring larger interpersonal distances across types of distances (see **Figure 1**). Sensitivity of peripersonal spaces to social aspects such as gender and age of the person approaching the participant, has also been stressed by Iachini et al. (2016). However, in our study, neither the gender nor age of the person approaching was specified and thus direct comparison of results is not possible. Our results are in line with the findings of Sorokowska et al. (2017) and we find their interpretation that women are more sensitive to social situations and tend to avoid dominant "invasions" of their personal space most likely.

With regard to geographical location (mainland/island), there was no significant main effect on preferred interpersonal distances. However, we found a significant interaction between geographical location and preference depending on the type of interpersonal distance: islanders preferred larger social distances than mainlanders, but there were no differences in preferred personal and intimate distances. This means that geographical location did not play a role in preferred distances from familiar and close persons—which we have already elaborated on earlier in the text. Furthermore, it should be noted that, along with other previously established variables (culture, social context, etc.) influencing preferred interpersonal distances, during a pandemic, there is a new element which should be taken into account. A recent study showed that wearing a mask reduces the subjective need for social distancing (Cartaud et al., 2020). In our particular task, however, this probably did not affect the results, as in spring 2020 mask wearing was practically non-existent in Croatia, with the exception of closed, public spaces, such as grocery shops, banks etc., mask wearing was neither mandatory nor recommended at the time.

How Did the COVID-19 Pandemic Impact our Behavioral Immune Systems?

To answer this, we compared the scores in BIS-related variables obtained in this sample with some of our earlier pre-pandemic samples. Not surprisingly, scores on all relevant variables (germ aversion, perceived infectability, pathogen disgust, and preferred interpersonal differences) were significantly higher in this sample (see **Tables 4, 5**). These findings are in line with recent findings by Miłkowska et al. (2021) who found elevated levels of disgust sensitivity among women in a pandemic sample as compared to a pre-pandemic sample, and Stevenson et al. (2021), who found similar shifts in pre-pandemic to pandemic scores in core disgust and only marginally in germ aversion among several student cohorts. Our results differ from theirs regarding perceived infectability, which is probably a consequence of sample structure: their samples comprised of much younger participants than ours, which might have influenced participant vulnerability perception during the pandemic, seeing that older people are objectively more vulnerable to the SARS-CoV-2 infection. Furthermore, it seems that the shift toward higher infectability in our sample was driven by male scores, as there was a significant gender × time interaction with men perceiving themselves to be more vulnerable than before the COVID-19 pandemic, and women did not. Considering that men are more vulnerable to SARS-CoV-2 infection (Krams et al., 2020, 2021), and more likely to develop a complicated clinical presentation this finding seems to yet again reflect an adaptive shift in threat perception among men. This is especially relevant considering that a similar pattern has been observed in SARS and Middle East respiratory syndrome infections (Falahi and Kenarkoohi, 2021). As for the other two BIS-related variables, we found no interaction, only main effects of gender and time: in both pre-pandemic and pandemic samples, women showed higher levels of pathogen disgust and germ aversion than men, which is also in accordance with earlier research on sex differences in disgust sensitivity (see Al-Shawaf et al., 2018) and both men's and women's scores shifted significantly as a function of the pandemic.

Many of the BIS-related variables are usually operationalized as relatively stable traits, but these findings further underscore the notion that ecological and contextual elements modulate the expression of BIS components. We did not change the regular instructions on any of these scales nor did we instruct our participants to answer how they feel regarding their germ aversion and possible contamination now, as compared to how they usually feel, and yet the average scores shifted significantly compared to pre-pandemic scores. However, it should also be noted that all of our samples included disproportionately more women than men, and since there is an abundance of earlier work showing that women have greater disgust sensitivity (Al-Shawaf et al., 2018), we re-ran the pre-pandemic/pandemic analyses separately for men and women, and showed that shifts toward higher scores in all three BIS-related variables remained stable for men. However, this greater proportion of women in our pandemic sample might have skewed the results of regression analyses. Future research should take this into consideration, since from our experience, online studies without incentives for participants usually result in greater proportion of women. Another possible limitation of such comparison is measurement invariance. Our preliminary analyses suggest that the factor structures of the BIS-related questionnaires are stable in time, but we plan to explore this problem in a larger data set in ongoing research.

CONCLUSION

In conclusion, we found that BIS variables contributed significantly to all dependent variables, including preferred interpersonal distances, social cognitions, and emotions. Those whose BISs were more reactive or those who felt higher levels of pathogen disgust, germ aversion, and perceived themselves as more likely to get infected, felt more negative emotions toward strangers, preferred to keep larger physical distances from them, as well as from acquaintances and close persons, and were more inclined to punish those who did not adhere to the social and official rules implemented in order to prevent the spread of COVID-19. Members of (semi)isolated populations, in this case islanders, likely express such avoidant tendencies more intensely, as they are more susceptible to infectious diseases, being less exposed to various viral vectors due to their lifestyle. Finally, even though our sample size does not allow us to draw any conclusions at the population level, average scores on all BIS measures have shifted toward significantly higher average scores, indicating the effects of globally heightened awareness of potential contamination cues in our environments and a sort of sensitization to pathogen threat. Observed together, these findings further corroborate the notion that the BIS is a highly contextually sensitive pathogen detection and avoidance system, at least partially underlying various social cognitions and patterns of interpersonal approach/avoidance motivations.

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 Ethics Committee of the Department of Psychology, UNIZG. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

IH: hypothesis, study design, data analysis, and drafting and writing the manuscript. AG: study design, data analysis, and writing the manuscript. GK: study design and recruitment of participants. All authors contributed to the article and approved the submitted version.

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Communication Across Maternal Social Networks During England's First National Lockdown and Its Association With Postnatal Depressive Symptoms

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Postnatal/postpartum depression (PND/PPD) had a pre-COVID-19 estimated prevalence ranging up to 23% in Europe, 33% in Australia, and 64% in America, and is detrimental to both mothers and their infants. Low social support is a key risk factor for developing PND. From an evolutionary perspective this is perhaps unsurprising, as humans evolved as cooperative childrearers, inherently reliant on social support to raise children. The coronavirus pandemic has created a situation in which support from social networks beyond the nuclear family is likely to be even more important to new mothers, as it poses risks and stresses for mothers to contend with; whilst at the same time, social distancing measures designed to limit transmission create unprecedented alterations to their access to such support. Using data from 162 mothers living in London with infants aged $\leq$6 months, we explore how communication with members of a mother's social network related to her experience of postnatal depressive symptoms during the first "lockdown" in England. Levels of depressive symptoms, as assessed via the Edinburgh Postnatal Depression Scale, were high, with 47.5% of the participants meeting a $\geq$11 cut-off for PND. Quasi-Poisson regression modelling found that the number of network members seen in-person, and remote communication with a higher proportion of those not seen, was negatively associated with depressive symptoms; however, contact with a higher proportion of relatives was positively associated with symptoms, suggesting kin risked seeing mothers in need. Thematic qualitative analysis of open text responses found that mothers experienced a burden of constant mothering, inadequacy of virtual contact, and sadness and worries about lost social opportunities, while support from partners facilitated family bonding. While Western childrearing norms focus on intensive parenting, and fathers are key caregivers, our results highlight that it still "takes a village" to raise children in high-income populations and mothers are struggling in its absence.

Keywords: postnatal depression, COVID-19, social distancing, lockdown, mothers, cooperative breeding, maternal social networks

INTRODUCTION

Postnatal or postpartum depression (PND/PPD) is the term given to a bout of Major Depressive Disorder which has onset during pregnancy or within 4 weeks of birth (APA, 2013), though in practice it is applied to depression occurring within the first year from birth (Stowe et al., 2005; Halbreich and Karkun, 2006; Skalkidou et al., 2012). PND had a pre-COVID-19 estimated prevalence ranging up to 23% in Europe, 33% in Australia, and 64% in the United States (Arifin et al., 2018). PND predisposes mothers to future bouts of depression (Solomon et al., 2000), and becomes chronic in 38% of women (Vliegen et al., 2014).

While the evolutionary, ultimate function of depression is still under debate (Nettle, 2004; Hahn-Holbrook and Haselton, 2014; Myers et al., 2016, 2017; Hagen and Thornhill, 2017; Raison and Miller, 2017; Rantala et al., 2018), PND is associated with costs for both mothers and their children. For example, it inhibits a mother's ability to care for herself and her infant (Downey and Coyne, 1990; Boath et al., 1998), and is associated with increased risks of a range of inflammation-related illnesses (Mykletun et al., 2009; Keicolt-Glaser and Glaser, 2002). PND is also associated with deficits in a range of children's cognitive, social, and physical developmental outcomes (Cogill et al., 1986; Gelfand and Teti, 1990; Murray and Cooper, 1997; Beck, 1998; Wright et al., 2006), mediated in part by poorer mother-infant relations (Beck, 1995; Murray et al., 1996; Murray and Cooper, 1997; Coyl et al., 2002; Moehler et al., 2006; O'Hara and McCabe, 2013) which may last a life-time (Myers and Johns, 2018). Maternal mental health has increasingly been on the public health agenda due to the physiological and psychological consequences for mother-infant dyads, but also because of fiscal concerns – with the long-term costs of maternal mental health issues in the United Kingdom alone is estimated at £8.1 billion per 1-year cohort of births (Bauer et al., 2014). The full impact of the ongoing COVID-19 pandemic on maternal mental health is yet to be determined, but a picture of increased PND prevalence is rapidly emerging (e.g., see Davenport et al., 2020; Hessami et al., 2020; Spinola et al., 2020; Thayer and Gildner, 2020; Wu et al., 2020). As waves of COVID-19 continue to occur, it is crucial to understand how mothers are being impacted and what might mitigate their exposure to PND risk factors – here we take an evolutionarily informed focus on one such key risk factor, low social support (Beck, 2001; Yim et al., 2015; Doyle and Klein, 2020).

From an evolutionary perspective it is perhaps unsurprising that social support plays a role in maternal mental health, as humans evolved as cooperative childrearers where mothers require allomaternal support from kin and non-kin for successful reproduction (Hrdy, 1999; Hill et al., 2011; Dyble et al., 2015; Page et al., 2017; Emmott and Page, 2019). While the sources and nature of support vary across cultures, allomother [i.e., caregivers other than the mother (Hrdy, 1999)] presence and investments are generally associated with better maternal-child wellbeing (Sear et al., 2003; Gibson and Mace, 2005; Sear and Mace, 2008; Sear and Coall, 2011; Meehan et al., 2014). Mothers with infants are hypothesised to be particularly dependent on allomaternal support due to the high direct care needs of infants (such as prolonged carrying and high feeding frequency) which conflict with other activities (Hrdy, 1999); indeed, the postnatal period is often acknowledged in public health literature as a "vulnerable time" for mothers where they require high levels of support (Barlow, 2015; Johnston-Ataata et al., 2018). In Western contexts, despite the nuclear-family and intensive parenting norms (Faircloth, 2014; Sear, 2017) where fathers are key allomothers (Emmott and Mace, 2015; Emmott et al., 2020), public health literature shows that wider social support remains important for a range for postnatal health indices including maternal mental health (Crockenberg, 1981; Raj and Plichta, 1998; Beck, 2001; Kinsey et al., 2014; Yim et al., 2015; Emmott et al., 2020).

The COVID-19 pandemic has created a situation in which support from beyond the nuclear family is likely to be even more important to new mothers, as it poses actual and perceived health-related risks and stresses for mothers to contend with. At the same time, social distancing measures designed to limit viral transmission created unprecedented alterations to their access to such support. On the 23rd March 2020, England entered its first "national lockdown" following the increasing spread of COVID-19, where the government imposed social distancing measures requiring that individuals stay at home (unless exercising, shopping for food, or seeking medical attention), closed non-essential businesses and childcare facilities/schools, and banned public gatherings of more than two people. These measures remained in full force for almost 3 months until 14th June 2020, and likely impacted the social interactions of postnatal mothers in two primary ways: Firstly, by limiting in-person contact beyond the household, many women were no longer allowed to see their own mothers and other family members, as three-generation households containing young children are rare in the United Kingdom (Pilkauskas and Martinson, 2014). Family members, particularly maternal grandmothers, have been identified as important sources of childcare and domestic help in the United Kingdom (Emmott et al., 2020), meaning lockdown likely reduced the availability of practical support for mothers. Second, as antenatal classes and mother-baby groups were either cancelled or moved online during lockdown, potential interactions between new "mummy friends" were likely prevented, particularly for women giving birth after lockdown commenced. As female social networks often change in the perinatal period, with new supportive connections built with other women at a similar stage of pregnancy or motherhood (Nolan et al., 2012; Strange et al., 2014), this likely led to reduced social network connections among mothers, curtailing peer support. Although the cooperative childrearing literature typically focuses on female kin as key supporters on the grounds of inclusive fitness, who provides support appears to be flexible (Sear, 2021). New mothers benefit from reciprocal exchange of mothering-related support acts with non-related women at a similar stage of motherhood (Price et al., 2018; Finlayson et al., 2020). While there is limited data available on maternal social networks, mummy friends are likely to be particularly important in Western contexts where individuals frequently live long distances from kin.

Overall, lockdown led to a notably "unusual" childrearing environment even in Western contexts with strong nuclear family norms, limiting mothers access to allomother support beyond the nuclear family. Others have argued that lockdown

measures would be highly detrimental for families with children (Arnot et al., 2020), particularly for mothers with infants (Doyle and Klein, 2020). Low social support, as noted, is known to increase the risk of PND, and social isolation also has strong links with depressive onset more generally (Lakey and Cronin, 2008). Therefore, it is crucial to understand the impact of social distancing measures on maternal mental health and the degree to which remote methods of communication are able to buffer against the detrimental consequences of reduced face-to-face contact. Here we explore how contact and communication within a mother's social network relates to her experience of postnatal depressive symptoms during the first national lockdown in England. We focus on the experience of mothers in London – the initial epicentre of COVID-19 in England. This is due to our pre-existing project on maternal social networks in London, which was adjusted with the announcement of a national lockdown to investigate the impact of social distancing measures on maternal postnatal wellbeing.

RESEARCH AIMS

Here we take an exploratory approach to understand how social support networks existed during England's national lockdown amongst London mothers, and their associations with postnatal depressive symptoms. Specifically, we explore: (Q1) Who did mothers keep in contact with during lockdown and how (in-person vs. remote communication)?; (Q2) Did characteristics of maternal social networks during lockdown vary by timing of birth in relation to lockdown?; (Q3) How did maternal social network characteristics and social communication during lockdown associate with self-reported depressive symptoms assessed via the Edinburgh Postnatal Depression Scale (EPDS; Cox et al., 1987)? We conduct a concurrent design mixed-method study (Leech and Onwuegbuzie, 2009) where quantitative and qualitative analyses were carried out at the same time. Using self-reported social network data, we quantitatively describe maternal support networks and analyse their associations with indicators of PND. In parallel, we thematically analyse open-text data from the survey to explore and understand the lived experiences of mothers with infants during England's first lockdown. Both studies were preregistered before analysis (Quantitative study[1] and Qualitative study)[2] and minor deviations from our preregistered methods are outlined in the **Supplementary Material 1**. Finally, we synthesise the quantitative and qualitative findings to provide further insight.

DATA

About the Survey

We use cross-sectional social network data from 162 London-based mothers with infants aged ≤6 months, collected in May–June 2020 (covering the first lockdown in England) using the formr online survey platform v.0.18.0 (Arslan et al., 2020). Postnatal depressive symptoms were assessed via self-report using the Edinburgh Postnatal Depression Scale (EPDS; Cox et al., 1987). The EPDS is the most commonly used screening tool for PND; it consists of ten items and gives a score out of 30, with a higher score indicating higher depressive symptoms. Participants were asked to report their personal social networks by listing everyone who is important to them, up to a maximum of 25 alters. For each alter, participants reported their age, gender, relationship, parental status, and age of their youngest child if relevant. They then reported who in their network they had seen in person, and who they had spoken to or messaged remotely (via phone, video calls, WhatsApp, Facebook, etc.) in the last few weeks. We also collected a range of demographic variables (See https://osf.io/k5whj/ for survey materials.) In total, the survey took around 15 min to complete.

Women were eligible to take part if they lived and gave birth in London, England, with a child aged 6 months or under at the time of the survey. We took an opportunistic approach to recruitment, advertising the study via social media platforms such as Facebook and Twitter (social networking sites). For Facebook, study adverts were posted on local mums/parents groups, local residents groups, and national baby groups. Studies have shown that social media survey recruitment can lead to an increased proportion of middle-class participants (Topolovec-Vranic and Natarajan, 2016). In order to track the age and educational background of women who were signing up (thereby allowing us to adjust recruitment strategy), eligible women were first required to register their interests on our study site; however, due to time constraints, all eligible women were eventually invited via email to complete the survey. Participants were given a £5 voucher upon completion of the survey as a token of thanks. Multiple entries were prevented using IP-address checks. Ethical approval for the survey was obtained from the UCL Research Ethics Committee (ref. 14733/002).

Sample Characteristics

Mothers in our sample ranged in age from 19 to 47 years (mean 34.6, SD 4.2); half were first-time mothers (50.6%), while for 40.1% of women their infant was their second, 7.4% their third, and 1.9% their fourth child. The mean age of focal infant at the time of survey was 110 days (SD 56.6), with 115 infants born before 23rd March 2020, and 47 born after. Males comprised 54.3% of infants. The majority (53.7%) of births were reported to be uncomplicated, 34.6% associated with self-defined minor complications, and 11.7% major complications. The majority of infants were white (71.0%), 23.5% were of mixed ethnicity, and 5.6% were of other ethnicities. Only two participants reported not having a partner. Thirty-four percent reported an annual household income before tax of £0–75K, 19.8% £75,001–100K, and 34.6% over £100k (10 participants reported not knowing or preferring not to say, nine did not respond; see **Supplementary Material** for a detailed breakdown); the financial situation of the household had become worse during the pandemic for 29.0% of participants. The majority (87.0%) of participants were not socially isolating (i.e., staying at home and not going out because they or a household member had coronavirus symptoms or were vulnerable/at high risk) at the time of the

[1]https://osf.io/cse4a
[2]https://osf.io/82bwj

TABLE 1 | Table shows a summary overall personal network characteristics of the sample, along with a summary of patterns of communication with network alters (*N* = 162).

Measure		Full sample			Time of birth in relation to 23rd March (before/after)		
		Range	Mean (SD)	Median	Range	Mean (SD)	Median
Overall network characteristics							
Total number of alters	*n*	1, 15	11.4 (6.8)	10	2, 25/1, 25	11.9 (6.9)/10.1 (6.3)	10/9
Kin	*n*	1, 15	4.6 (2.5)	4	1, 15/1, 14	4.7 (2.5)/4.5 (2.5)	4/4
Mummy friends	*n*	0, 10	1.9 (2.2)	1	0, 10/0, 9	2.2 (2.3)/1.3 (1.9)	1/1
Seen in person in the last few weeks							
Total number of alters	*n*	1, 14	3.9 (2.9)	3	1, 14/1, 11	3.9 (2.9)/4.0 (2.7)	3/3
	%	4.5, 100	40.9 (26.2)	33.3	4.5, 100/10.0, 100	38.7 (24.8)/46.4 (29.1)	33.3/40
Kin	*n*	1, 10	2.3 (1.6)	2	1, 10/1, 7	2.3 (1.6)/2.4 (1.7)	2/2
	%	10, 100	57.2 (31.6)	50	10, 100/14.3, 100	55.7 (31.0)/61.0 (33.2)	50/50
Mummy friends*	*n*	0, 5	0.5 (0.9)	0	0, 5/0, 4	0.6 (1.0)/0.4 (0.8)	0/0
	%	0.0, 100	31.2 (36.8)	20	0.0, 100/0.0, 100	30.9 (36.2)/32.1 (39.4)	20/5.6
Communicated with remotely in the last few weeks							
Total number of alters	*n*	1, 25	10.8 (6.4)	10	1, 25/1, 23	11.4 (6.6)/9.4 (5.6)	10/8
	%	50.0, 100	95.4 (8.9)	100	50, 100/61.1, 100	95.6 (8.7)/95.0 (9.4)	100/100
Kin	*n*	0, 15	4.4 (2.5)	4	0, 15/0, 9	4.5 (2.6)/4.1 (2.1)	4/4
	%	0.0, 100	94.5 (15.9)	100	0.0, 100/0.0, 100	95.2 (15.2)/92.9 (17.4)	100/100
Mummy friends*	*n*	0, 10	1.8 (2.1)	1	0, 10/0, 8	2.1 (2.2)/1.2 (1.8)	1/1
	%	42.9, 100	98.0 (9.1)	100	42.9, 100/88.9, 100	97.4 (10.4)/99.6 (2.2)	100/100
Communicated remotely but not seen in the last few weeks							
Total number of alters	*n*	0, 22	7.1 (5.3)	6	0, 22/0, 14	7.7 (5.6)/5.7 (4.0)	6/5
	%	0.0, 100	56.9 (25.8)	60	0, 100/0, 90	59.3 (24.5)/51.0 (28.2)	64.3/57.1
Kin	*n*	0, 11	2.3 (2.2)	2	0, 11/0, 6	2.4 (2.3)/1.9 (1.9)	2/2
	%	0.0, 100	42.3 (32.0)	50	0.0, 100/0.0, 100	44.1 (31.2)/37.9 (33.8)	50/33.3
Mummy friends*	*n*	0, 8	1.3 (1.6)	1	0, 8/0, 7	1.5 (1.8)/0.9 (1.5)	1/0
	%	0.0, 100	66.8 (37.7)	75	0.0, 100/0, 100	66.5 (37.4)/67.5 (39.2)	75/88.9

**Sample size for percentages is 107 as some participants reported no mummy friends.*

survey. For a detailed breakdown of sample characteristics see **Supplementary Material 2**.

The full social network characteristics of participants can be seen in **Table 1**; on average, participants' personal networks contained 11 alters, composed of 47.8% kin and 14.7% mummy friends (female non-kin with infants aged 18 months or under).

Levels of depressive symptoms were high in our sample. Typically, EPDS scores in the general population are heavily skewed to the lower end of the scale (Alvarado et al., 2015; Coll et al., 2017; Martin and Redshaw, 2018; Smith-Nielsen et al., 2018; Boran et al., 2020); however, in our sample, they approximated a normal distribution with a mean of 10.4 (SD 4.7) (**Figure 1** and **Supplementary Figure 1**). While comprehensive descriptive statistics of EPDS scores are rare in the literature, a pre-pandemic mean of 6.4 (SD 6.9) has been reported for English mothers at 3 months post-birth (Martin and Redshaw, 2018) and one of 7.2 (SD 4.4) among first-time Irish mothers at 6 weeks post-birth (Leahy-Warren et al., 2012). Our sample EPDS scores are therefore relatively high, and this elevation appears similar for women giving birth before 23rd March (mean 10.7, SD 4.9) and after (mean 9.9, SD 4.4), with little evidence of a correlation with days since birth (**Supplementary Figure 3**). A recent meta-analysis of EPDS usage recommends a cut-off of ≥11 to identify most women who would meet diagnostic criteria for PND and ≥13 for those with higher symptom levels (Levis et al., 2020); in our sample 47.5% and 34.6% of women, respectively, met these criteria for PND.

QUANTITATIVE ANALYSES OF SURVEY DATA

Quantitative Analyses Methods

Here we address the questions: (Q1) Who did mothers keep in contact with during lockdown and how (in-person vs. remote

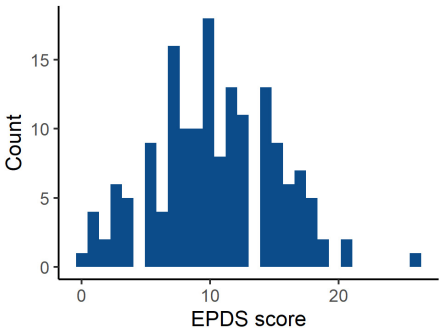

FIGURE 1 | Histogram showing the distribution of Edinburgh Postnatal Depression Scale (EPDS) scores (*N* = 162).

communication)?; (Q2) Did characteristics of maternal social networks during lockdown vary by timing of birth in relation to lockdown?; and (Q3) How did maternal social network characteristics and social communication during lockdown associate with Edinburgh Postnatal Depression Scale scores?

To address Q1, we quantitatively described social network characteristics and patterns of communication with network members. We also quantified the number and percentage of participants having either in-person or remote communication with the following key supporters: their own mother, their partner/infant's father's mother, a mummy friend. We also report *post hoc* exploration of in-person communication with kin by type (i.e., consanguineal vs. affinal), to shed light on findings in relation to Q3.

To address Q2, we examined differences in the aforementioned network characteristics by timing of birth, plotting the data and visually inspecting the distributions for changes in the pattern of social networks around the 23rd March when lockdown was imposed – which would be suggestive of a lockdown-specific effect. We took an exploratory approach rather than making predictions, because while the imposition of lockdown is a clearly defined event, it is possible that increasing public awareness led to behavioural alterations in the weeks before lockdown and/or any impacts of lockdown took time to develop. Secular trends may also be potentially attributable to lockdown, but with this data alone we are unable to disentangle them from infant age effects.

To address Q3, we used quasi-Poisson regression models to test for a relationship between social communication and EPDS scores. We anticipated seeing social contacts in person would have more of a protective effect on mental wellbeing than communicating with them remotely; thus, a first set of models assessed whether the number and/or percentage of (i) all alters, (ii) kin, and (iii) mummy friends seen in person (our independent variables) predicted EPDS score (our dependent variable). The *number of alters seen* reflects a mother's in-person social network size during lockdown, capturing the number of people mothers have actually seen within their "network of important people" in the few weeks prior to the survey. While we do not have pre-pandemic data on maternal social networks, given the known relationship between closeness and in-person contact (e.g., Roberts and Dunbar, 2011), we interpret *percentage of alters seen* to reflect the extent to which mothers maintained in-person contact within their personal networks of important people during lockdown (i.e., of the important people in their lives, what proportion did mothers see in-person). To clarify, mothers could report a small *number of alters seen,* indicating a small lockdown in-person network, but report a high *percentage of alters seen*, indicating that they maintained in-person contact with a high proportion of important people in their lives. A second set of models were then used to assess whether having remote communication with those not seen, either as the absolute number or percentage of (i) all alters, (ii) kin, and (iii) mummy friends (our independent variables) predicted EPDS score (our dependent variable).

Model selection (outlined briefly below and in detail in the **Supplementary Material 1**) was performed between the following potential confounds influencing PND risk and/or social network characteristics to determine the control variables in our models: remote communication with social contacts, network size, partnership status, age of the mother, age of the infant, birth complications, infant sex, parity, has financial situation become worse since COVID-19, socially isolating at time of survey, infant's ethnicity, household income, and time of birth in relation to lockdown.

Our model selection strategy was preregistered before exploratory analyses were conducted and stemmed from the base directed acyclic graphs (DAGs) in **Supplementary Figures 2A,B**, from which we used the R package dagitty (Textor et al., 2016) to select our control variables; the rationales for the relationships between our variables assumed in these DAGs are outlined in **Supplementary Material 1**. We ran a single control variable selection process using data relating to all alters, assuming the communication variants for (i) all alters, (ii) kin, and (iii) mummy friends share relationships with our potential confounds. From this starting point, we first updated the base DAGs based on the sample characteristics determined by exploratory analysis, and then assessed whether the implied conditional independencies from these updated DAGs were supported by the data (McElreath, 2020). Where independence was not supported, we updated our DAGs accordingly and repeated assessment of the newly implied conditional independencies until no updates were required (an overview of this process and the final DAGs can be found in the **Supplementary Material 1**; for full details see the R code available at https://osf.io/sr6d5/). We then selected the smallest minimally sufficient adjustment sets to adjust for in our models. We interpret the *number of alters seen* to reflect in-person network size during lockdown, and *percentage of alters seen* to reflect maintenance of in-person contact within personal networks during lockdown. We made no explicit prediction as to whether the *number* or the *percentage* of alters seen would be more important for predicting postnatal depressive symptoms; as a result, model selection produced two adjustment sets, one for when the independent variable of interest or exposure was the number of alters seen and one for when the exposure was the percentage of alters seen, equating to 12 models.

The variables retained in model selection were used as follows (for details of the variable derivation see the **Supplementary Material 1**): Independent variables: *in-person communication – number* was a continuous measure of the total number of (i) all alters, (ii) kin, or (iii) mummy friends seen in the last few weeks; *in-person communication – percentage* was a continuous measure of the percentage of (i) alters, (ii) kin, or (iii) mummy friends seen in the last few weeks; *remote communication but not seen – number* was a continuous measure of the total number of (i) alters, (ii) kin, or (iii) mummy friends communicated with remotely but not seen in the last few weeks; *remote communication but not seen – percentage* was a continuous measure of the percentage of (i) alters, (ii) kin, or (iii) mummy friends communicated with remotely but not seen in the last few weeks. Control variables: *age of infant*, measured in days, was used continuously; *age of mother*, measured in years, was used continuously; *parity* was used as a binary categorical variable

of "1" (reference) vs. "2 or higher," *household income* was used as a binary categorical variable of "£0–100K" (reference) or "over £100K," *socially isolating* was used as a binary categorical variable of either "yes" or "no" (reference); *infant's ethnicity* was used as a binary categorical variable of either "white" (reference) or "non-white."

Results of Quantitative Analyses

Q1: Who did mothers keep in contact with during lockdown and how (in-person vs. remote communication)?

On average, women had seen one family member other than their partner, three alters in total, and no mummy friends in the last few weeks (**Table 1**), while levels of remote communication were high across all categories of network alters. The majority (79.0%) of mothers in our sample reported their own mother as part of their personal network; of those, 49.2% had seen their mother in the last few weeks and 99.2% had communicated remotely with her (38.9 and 78.4% of all participants, respectively). Participants reported a median of 3 consanguineal kin (range 0–11) and 1 affine (range 0–6). While on average participants reported seeing the same number of kin across kin type (consanguineal and affinal: median 1, range 0–6), patterns within this differed. Forty-seven and a half percent of mothers had seen none of their own relatives, 17.9% had seen one, 19.1% had seen two, and 15.4% had seen three or more, with 25.3% seeing all their named consanguineal kin. On the other hand, 1.2% had seen no affines (the two single mothers in the sample), 8.0% had seen two affines, 4.3% had seen three or more, with the remaining 86.4% having seen one, i.e., only their partner, with 78.1% seeing all of their named affines. Only 19.8% of mothers listed their partner's mother; of those 37.5% had seen her and 100% had communicated remotely (7.4 and 19.8% of all participants, respectively). The majority (66.0%) of participants reported having at least one mummy friend; of those, 54.2% had seen a mummy friend in the last few weeks and 100% had remote communication (35.8 and 66.0% of all participants, respectively). Weak (<0.3) to moderate ($0.3 \geq r < 0.7$) positive correlations were found between the *number* and *percentage* of alters seen across categories, while correlations between the *number* and *percentage* remotely communicated with were weakly positive for all alters and kin and weakly negative for mummy friends (**Supplementary Material 1**).

Q2: Did characteristics of maternal social networks during lockdown vary by timing of birth in relation to lockdown?

We found only limited evidence of differences in the overall network characteristics of participants, dependent on whether they gave birth before or during lockdown (plots by date of birth can be seen in **Supplementary Figures 4–14**), with some indication that women giving birth on or after March 23rd had fewer mummy friends (**Table 1** and **Figure 2A**). We found some indication that patterns of communication with mummy friends also differed between mothers giving birth since lockdown commenced to those giving birth before, with those giving birth since being less likely to have seen their mummy friends (**Figure 2B**) but more likely to have communicated with them remotely if they had not seen them (**Figure 2C**).

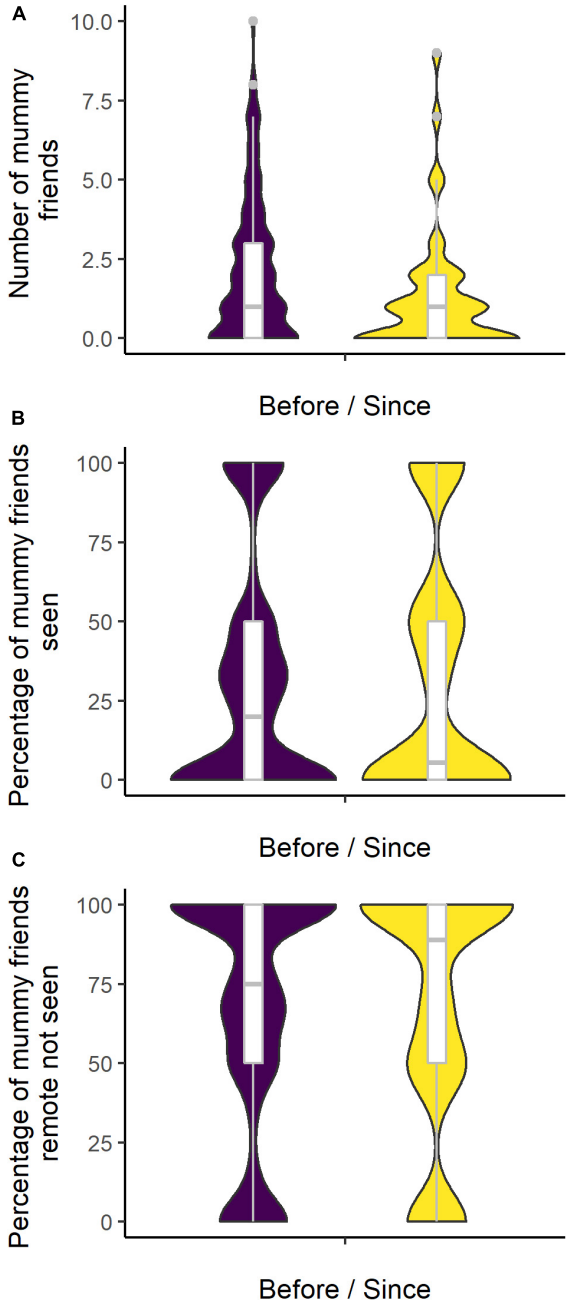

FIGURE 2 | (A–C) Violin plots show the density distribution of network characteristics in relation to mummy friends by timing of birth, with in-set box plots showing the median and interquartile range [**(A)** $N = 162$; **(B,C)** $n = 107$].

Q3: How did maternal social network characteristics and social communication during lockdown associate with Edinburgh Postnatal Depression Scale scores?

Here we present the quasi-Poisson regression models with the largest adjusted R^2s (referred to as Models 1–3 for ease of interpretation – **Table 2**), while the remaining models performing better than chance can be seen in **Supplementary Material 2**; comparison of quasi-Kullback Information Criterion (QKIC)

TABLE 2 | Results of quasi-Poisson regression models predicting depression symptoms as assessed via the Edinburgh Postnatal Depression Scale (EPDS) (n = 153).

Variables	Coef	SE	RRR	LCI	UCI
Model 1: All alters – in person communication (% as exposure)					
(Intercept)	2.405	0.172	11.078	7.897	15.475
In person communication (all alters) – %	**0.002**	**0.002**	**1.002**	**0.999**	**1.005**
Age of infant	0.001	0.001	1.001	0.999	1.002
Infant's ethnicity – non-white	0.044	0.082	1.045	0.889	1.225
Household income – over £100k	−0.054	0.075	0.948	0.817	1.098
In person communication (all alters) – no.	**−0.036**	**0.015**	**0.965**	**0.937**	**0.993**
Socially isolating – yes	0.003	0.114	1.003	0.799	1.248
Variance-function-based R^2					0.121
Variance-function-based R^2 – adjusted					0.085
Model 2: Kin – in person communication (% as exposure)					
(Intercept)	2.178	0.173	8.833	6.275	12.384
In person communication (kin) – %	**0.003**	**0.001**	**1.003**	**1.001**	**1.006**
Age of infant	0.001	0.001	1.001	0.999	1.002
Infant's ethnicity – non-white	0.067	0.081	1.069	0.911	1.250
Household income – over £100k	−0.040	0.076	0.961	0.828	1.114
In person communication (kin) – no.	**−0.026**	**0.027**	**0.975**	**0.924**	**1.026**
Socially isolating – yes	0.075	0.110	1.078	0.865	1.331
Variance-function-based R^2					0.117
Variance-function-based R^2 – adjusted					0.081
Model 3: All alters – remote communication but not seen (% as exposure)					
(Intercept)	2.732	0.168	15.365	11.007	21.280
Remote communication but not seen (all alters) – %	**−0.005**	**0.002**	**0.995**	**0.991**	**1.000**
Age of infant	0.001	0.001	1.001	0.999	1.002
Household income – over £100k	−0.057	0.075	0.944	0.815	1.093
In person communication (all alters) – no.	**−0.051**	**0.017**	**0.950**	**0.918**	**0.983**
Remote communication but not seen (all alters) – no.	**0.013**	**0.011**	**1.013**	**0.992**	**1.034**
Socially isolating – yes	0.006	0.112	1.006	0.803	1.248
Variance-function-based R^2					0.140
Variance-function-based R^2 – adjusted					0.105

Coef, coefficient; SE, standard error; RRR, relative risk ratio; LCI, 95% lower confidence interval; UCI, 95% upper confidence interval; no., number. Independent variables of interest are in bold.

values indicated no clear "best" model (Burnham et al., 2011; Kim et al., 2013). As anticipated, the overall number of network alters seen in person over the last few weeks negatively predicted depressive symptoms, with the relative risk ratios (RRRs) ranging from 0.950 to 0.974 across models (Model 1 in **Table 2**, also see **Supplementary Material 2**). Once the number of alters seen was accounted for, contrary to expectations, point estimates for the proportion of the network seen had a positive association with depressive symptoms, a finding that appears to be driven by the effect of kin: The RRR for the percentage of network alters seen (Model 1) was 1.002 (CI 0.999, 1.005) and for kin (Model 2) 1.003 (CI 1.001, 1.006), and while the confidence intervals overlapped one for all alters, they narrowed when looking specifically at kin – this may be indicative of relatives being more likely to visit mothers in greater distress. *Post hoc* single variable models containing just the percentage of network alters seen found the direction of this effect to be the same when not controlling for number seen (see **Supplementary Material 2**). Finally, as anticipated, the greater the percentage of all alters communicated with remotely, if not seen in person, also appeared to be associated with lower depressive symptoms (Model 3) (RRR = 0.995, CI 0.999, 1.000); this pattern was repeated for the percentage of kin (RRR = 0.996, CI 0.991, 1.001), though with upper bound confidence intervals just overlapping one (see **Supplementary Material 2**). Models looking at mummy friends specifically did not perform better than chance (results not shown); this seems likely to be due to the widespread low levels of contact with other mothers with infants, with 55 participants reporting no mummy friends in their networks and on average mothers only reporting one. Note, our models varied in their performance and captured only limited variance in EPDS score, suggesting unaccounted for factors were playing an important role in maternal wellbeing, which is unsurprising.

QUALITATIVE ANALYSIS OF SURVEY DATA

Qualitative Analysis Methods

To complement the quantitative analysis and help with overall inference, we conducted an inductive thematic analysis of open-text survey responses. In our survey, we asked three

open-text questions: (Q1) "Is there anything you would like to share about how you feel the COVID-19 pandemic has affected your emotional relationship with your baby(ies)?" (Q2) "Is there anything you would like to share about how you feel the COVID-19 pandemic has affected your emotional wellbeing?" and (Q3) "Before you finish the survey, we would like to hear about anything else you feel is important to your experiences at this unusual and difficult time. If you have any other thoughts you would like to share, please do so below." Questions therefore directed participants to elaborate on bonding with their baby(ies), their emotional wellbeing, and any other important matters they wished to raise. Of the 162 women who took part in the survey, 122 participants (75%) provided a response to one or more open-text questions, with 96, 82, and 77 participants responding to Q1, Q2, and Q3, respectively. Note, while these three questions were posed separately, the responses to these questions do not exist independently: For example, participants may refer back to their response in Q1 while responding to Q2, or decide to skip Q3 as they expressed all they wanted to in the earlier questions. This meant responses could not be analysed by question. In total, our data included 256 open-text responses with 61 words on average per response.

One of us (EE) conducted an inductive thematic analysis of open-text survey responses using NVivo v12. First, 96 open-text responses were coded in detail by EE and emerging themes were identified. Coding saturation was experienced early on at around 50 cases, implying relative similarity in the content of participant responses. EE then separately discussed emerging themes with SM and a subject-equivalent (new mother resident in London), and sought feedback on interpretation. Following discussion, EE amended the themes and coded all participant responses, with negative case analysis (i.e., specifically looking for participant responses which did not fit pre-specified themes). As a final validation step, as EE and SM do not have direct experiences of motherhood, EE and SM discussed findings with two mothers who had experienced lockdown with their infants to ensure findings were plausible. To minimise interpretive bias, the qualitative analysis method was designed and pre-registered in advance of any reading of participant responses (see text footnote 2) and was conducted parallel to the quantitative analyses by SM (i.e., results from quantitative findings were unknown at the time of qualitative analysis). Further information on the analysis process is outlined in the **Supplementary Material 1**.

The current method, combined with the characteristics of available data, was designed to identify underlying themes in the collective experiences of participants. As an exploratory, inductive design, we did not ask specific questions related to pre-existing ideas or hypotheses. Further, as open-text survey responses are relatively short, they are unlikely to provide a comprehensive description of maternal experiences during lockdown. This means that participants *not* raising certain experiences in their responses did not mean they lacked those experiences; therefore, our findings describe sample-level rather than individual-level characteristics. While we are unable to translate the findings to individual-level descriptors of maternal experience, our study nonetheless provides insight into the different types of experiences mothers in London encountered during the first national lockdown.

Results of Qualitative Analysis

We identified four themes in our participant responses: One theme relating to the "benefits of lockdown" and three themes relating to the "costs of lockdown" (**Table 3**). These themes are not mutually exclusive and could have been experienced in different combinations, although the extent to which they overlap is unclear from our current study. The descriptions of each theme and example quotes are outlined below. More example quotes are available in the **Supplementary Material 1**.

Theme 1: Enhancing Bonding With Baby Within the Nuclear Family

For some women, lockdown gave them an unexpected opportunity to increase the "quality time" spent with the baby as a family, leading to perceived better bonding, improved relationships within the nuclear family, and positive emotional wellbeing. The stay-at-home and social distancing orders "protected" the nuclear family from visitors and non-essential commitments, leading to uninterrupted time and the ability to devote attention to the baby. Often, this was accompanied by high partner involvement, co-parenting, and practical support: As more people worked from home or were furloughed, partners were able to substitute maternal care allowing mothers to "take some time" and invest in themselves – such as catching up on sleep or exercise.

> *"At first I was afraid that not being able to have any help might effect my relationship but in [fact] it has made it so strong because I've been with her all the time. . . .I have enjoyed the closeness and my son becoming closer to his baby sister."*

> *"The lockdown has been a big positive for my connection with the baby. I have been able to relax and enjoy her and give her my undivided attention versus [needing] to rush around, see people/host people etc. It has also been a great help having my partner home every day as it means most days I can get at least 1 h to myself which I use to exercise or catch up on sleep. . . .Also I think it has been an amazing positive on my partners ability to build a bond with the baby and co-parent."*

Theme 2: The Burden of Constant Mothering

In stark contrast to the benefits of lockdown, many women also raised the burden of "constant mothering" due to the sudden severing of practical support. With no alloparents available to provide practical support and having to "do it alone," mothers experienced the intensification of domestic and caregiving tasks. While the availability of partner support was not always clear, several women shared that their partners were not readily available to provide practical support due to work conflicts. This left mothers feeling exhausted and isolated, with no time to rest or recuperate, and some women reported feeling overwhelmed at the responsibility of looking after their child(ren) on their own. Particularly for mothers with multiple children, the lack of childcare and school closures meant women experienced competing demands for attention. This led women to experience

TABLE 3 | Summary of themes and key findings from our qualitative analysis.

	Main themes	Key findings
Benefits of lockdown	1. Enhancing bonding with baby within the nuclear family	Lockdown leading to uninterrupted time and "protection" of the nuclear family, leading to better bonding Facilitated by high levels of practical support from the partner
Costs of lockdown	2. The burden of constant mothering	Lack of practical support and childcare leading to the intensification of domestic and caregiving tasks Increased feelings of exhaustion and guilt
	3. Inadequacy of virtual contact	The lack of "incidental support" with virtual contact Lack on information transmission and affirmative support leading to low maternal confidence
	4. Lost opportunities	Inability to expand mother-infant social networks Feelings of sadness for lost experiences, for both mum and baby Worries about baby's development due to lack of physical contact with others

guilt that they could not provide enough attention to their baby, with a few women expressing a sense of resentment toward their children and worsening family relationships. Overall, mothers were forced to devote their time to motherhood, and the ability to invest in other aspects of their lives including themselves and their relationships were severely restricted.

> *"I think lockdown has made me feel like I'm not a person in my own right anymore, just a mum which is a feeling I had early on after my son was born but which disappeared when he was a few months old. Not having anyone else to hold him or help out a bit makes me feel it's all me and it's a lot of pressure which I can resent. I feel like I don't have any time to rest."*

> *"Being able to just pass my baby round the loved ones would give me moments to enjoy without her, in the knowledge she was being stimulated and cared for by others. Without that it's in a much smaller group of people to do that that leaves each of us far less time to focus on ourselves. I certainly miss being able to have people over and just hand them my baby so I can take 5 min to be [on] my own. I've only managed to be really alone once since she was born. Similarly, I've only once had 20 min with my partner without my baby being under our direct care since she was born that makes it hard for us to foster our connection. My mum does help but often we all sit together. I think without COVID I'd have more people offer to take her round the block and give us these moments of calm."*

Theme 3: Inadequacy of Virtual Contact

During lockdown, many women relied on social media and remote communication methods such as WhatsApp and Zoom to keep in touch with others. A small number of mothers explicitly mentioned they have been able to maintain or even increase contact with others via remote communication methods, which served as important sources of support. However, many women commented on the inadequacy of virtual contact which led to a sense of isolation as well as worries and anxieties. Notably, mothers expressed that remote communication did not allow for unplanned and unsolicited support, where supporters incidentally identify maternal or infant needs and provide spontaneous reassurances or help. Without face-to-face contact, family, friends, peers, and health professionals could not "see the whole picture" regarding mothers and their infants, meaning mothers had to actively raise issues and seek support. This was particularly challenging for mothers who felt uncomfortable about asking for support or had low self-efficacy, leaving them with unmet support needs.

> *"I'm the sort of person that doesn't like to ask for help, and therefore relies on face to face contact to comfort and support me. I feel like the support I have has diminished now that I'm not able to have close contact with anyone outside my household. . ."*

Beyond support, the lack of face-to-face contact also acted as a barrier for information transmission to mothers from peers and health professionals. With fewer opportunities for "general chats" where women could raise minor questions or concerns, some women described their uncertainties around their parenting and baby's development. Overall, this overlapped with increased anxiety and lower maternal confidence.

> *"I joined a baby group and was hoping to get to meet up and share stories and learn how to be a mom from them and that [hasn't happened]. I feel very like I am making it up as I go along and have no one to guide me as the health visitor can't visit either. It is hard."*

> *"Your questions ask if I've had emotional support – yes, lots of communication and video calls. But during lockdown we were completely physically isolated which made us very stressed and anxious with no one to give practical advice on general parenting."*

Theme 4: Lost Opportunities

Many mothers expressed their sense of sadness and grief in relation to lost opportunities with other people. In particular, women mourned the loss of "mummy friends," as closing of parent-baby spaces and classes meant mothers were not able to establish new friendships for themselves and their babies as anticipated. Some mothers explained that this meant they had less access to peer support and advice. Further, several mothers mourned the loss of sharing "special moments" with family members, with specific concerns around the inability to establish bonds and connections between the baby and wider family.

> *"This isn't how I saw my experience with my first baby and sometimes it almost feels like grieving for an experience that we won't get back. She is a beautiful baby and we are so lucky to have her. I wish I could share her and also actually discuss face to face with people what it is like being a mother – which they would be able to see physically."*

> *"You're only a first time mum once, and I was really looking forward to this time and making new mum friends. I think I am most sad about missing out on that."*

Many mothers believed these lost opportunities led to a sub-optimal developmental environment for the baby. In particular,

mothers were worried that the lack of social experiences might negatively impact their baby's long-term development. Mothers felt face-to-face contact with wider family and other babies were crucial for their development, which could not be adequately substituted by video calls. This was accompanied by a sense of guilt and worries about "over-attachment".

> *"I have a lot of worry about the developmental impact this will [have] on my son- I have already noticed he is more needy and although we regularly FaceTime them, I worry he won't recognise my family members very well when lockdown is lifted. He seems to have developed physically and mentally so much in the last few months that It makes me worry more."*

> *"I feel so guilty that he will not be able to play with other children and worry how it will affect him."*

SYNTHESIS OF QUANTITATIVE AND QUALITATIVE FINDINGS

Our sample of London mothers with infants exhibited high levels of depressive symptoms, with the mean self-reported EPDS score being 10.4, just 0.6 points below the recommended lower cut-off of 11 points to identify women who may meet the diagnostic criteria for PND (Levis et al., 2020). Forty-seven and a half percent of participants met the ≥11 cut-off for PND, and 35% of participants met the higher ≥13 cut-off for PND. The high levels of depressive symptoms in our sample were further supported by the themes arising in our open-text responses, with many women raising feeling stressed, anxious, and worried, as well as experiencing feelings of loneliness and sadness – overlapping with symptoms of PND (Cox et al., 1987; APA, 2013). Many women further reported they experienced a burden of "constant mothering" which left them physically and emotionally exhausted (Theme 2).

Lockdown Network Size and Depressive Symptoms

Our quantitative results showed that, unsurprisingly, in-person contact during lockdown was low, with mothers typically seeing one family member other than their partner in the last few weeks. At the same time, levels of remote communication were high across maternal social networks. Contacting others in-person and remotely were both associated with lower EPDS scores, suggesting social network size during lockdown was associated with lower PND risk. Our qualitative findings highlight that in-person contact is important for practical support (Theme 1 and 2), as well as effective information transmission and emotional support (Theme 3), suggesting that mothers with higher levels of in-person contact may have been able to access more better-quality support, leading to lower depressive symptoms. However, our qualitative findings also revealed that the experience of remote communication was often felt as inadequate (Theme 3), somewhat conflicting with our quantitative findings. Taken together, our results perhaps reflect that, while remote communication is "not as good" as in-person contact, it could still bring some potential benefits; and remote contact may be better than no contact in mitigating depressive symptoms.

Kin Support and Depressive Symptoms

While social network size during lockdown was associated with lower PND risk, proportionally higher in-person contact with kin network members - reflecting greater maintenance of their "important" kin network during lockdown - controlling for number of kin seen was associated with higher EPDS scores. Some of the cooperative childcare literature has noted differential impacts by kin type, with affinal kin sometimes found to be less beneficial and/or detrimental [most notably in relation to child outcomes (Sear and Mace, 2008)]. However, given the lack of variance in in-person contact with affinal kin, with most mothers only seeing their partner, our results appear to be driven by variations in contact with own kin. While our qualitative findings did not reveal the exact mechanism behind this association, the importance of practical support and in-person contact emerged as key components of maternal experience across multiple themes (Theme 1, 2, and 3). With this, one would expect in-person contact to associate with lower EPDS scores. A possible interpretation of our unexpected quantitative result is that, assuming in-person support is a more effective form of support (Theme 3), important kin members may have been more inclined to maintain in-person contact to support mothers experiencing PND symptoms. In-person contact did not only come with COVID-19 infection risk: it also risked fines (BBC News, 2020a) as well as public shaming and reputational damage (BBC News, 2020b). Kin members identified as important by mothers, given their relatedness and closeness, may have been more willing to take on these risks and potential costs to support mothers in need. However, it could also be that in-person communication with family members under socially distanced conditions served as a reminder of how much help mothers needed and/or were missing out on, thereby creating or exacerbating emotional distress. Indeed, mothers raised how lost opportunities for socialisation and support led to feelings of sadness (Theme 4).

Peer Support and Depressive Symptoms

We found weak evidence that mothers who gave birth during lockdown had fewer "mummy friends" (i.e., female friends with young infants) compared to those who gave birth before. Further, we did not find evidence that contact with mummy friends was associated with lower depressive symptoms. This may be due to the lack of variation in the number of mummy friends reported by participants: On average, mothers in our sample reported just one mummy friend, with 55 participants reporting none. Nonetheless, our qualitative analysis revealed the potential importance of mummy friends, with mothers "mourning" the lost opportunities to make friends which could lead to maternal anxieties (Theme 4). Mothers also reported receiving lower levels of support and information from peers due to the inadequacy of virtual communication (Theme 3). Mothers indicated that in-person contact with peers is key for information transmission and affirmative support – which, in "non-COVID-19" times, would have helped women develop maternal capital in the form of parenting knowledge, skill, and confidence. It may be that

mummy friends were not necessarily identified as "important people" within maternal social networks; alternatively, it may be that the pandemic has impeded the development of nascent mother-mother bonds in mothers giving birth prior to lockdown too, as well as their initial creation, leaving a wider cohort of women with few maternal social contacts. It is also worth noting that we used a narrow definition of mummy friends, limiting it to those currently with young children; it is more than likely mothers received support from friends at other stages of life too. Either way, peers may still be an important source of information and support – a resource mothers had limited access to during lockdown. Indeed, maternal support interventions in England and other developed populations often rely on organised peer support, with some evidence that this is associated with lower depressive symptoms (Leger and Letourneau, 2015).

DISCUSSION

Taking the quantitative and qualitative findings together, our results provide an in-depth description of maternal social networks during lockdown and its potential impact on depressive symptoms among the London mothers in our sample. The first national lockdown in England during the COVID-19 pandemic led to a childrearing environment which greatly minimised contact between households, curtailing access to support networks which typically provide allocare and other forms of social support (Emmott et al., 2020; Myers et al., 2021). In these arguably unusual times, our sample of London mothers with infants exhibited high levels of depressive symptoms with the mean EPDS score of 10.4 points. Forty-seven and a half percent of participants met the ≥11 cut-off for PND, and 35% of participants met the higher ≥13 cut-off for PND. This is notably higher than the pre-pandemic estimated PND prevalence of up to 23% in Europe (based on various measurement tools and cut-offs) (Arifin et al., 2018), but in line with other studies on maternal mental health during the COVID-19 pandemic. For example, recent studies conducted during the pandemic found 49% of mothers in a United Kingdom sample (Harrison et al., 2021), 33.2% in a Canadian sample (Cameron et al., 2020), and 23.6% in a Belgian sample (Ceulemans et al., 2020) met the ≥13 cut-off for EPDS scores, and 44% in an Italian sample met a ≥12 cut-off (Spinola et al., 2020). Multiple pre- vs. during-pandemic studies have also found increased prevalence of depressive symptoms (Wu et al., 2020; Zanardo et al., 2020); for example, a Canadian study found a jump from 15 to 40.7% of mothers meeting a ≥13 EPDS cut-off (Davenport et al., 2020). Combined with studies documenting elevated postnatal stress and anxiety (for example, see: Cameron et al., 2020; Ceulemans et al., 2020; Harrison et al., 2021), and more generalised measures of emotional wellbeing (Dib et al., 2020), there appears to be a broad picture of maternal emotional suffering on a wider scale than would be expected pre-pandemic.

It has been proposed that "depression is an adaptation designed to detect the opportunity costs of cooperative ventures and to subsequently bargain for increased benefits" (Hagen, 2003: 115). Under this framework, PND is argued to arise when the mother's circumstances are such that withdrawing investment in their infant in the hope of eliciting support from others is the least bad option (Hagen, 2003). An alternative line of reasoning – the Pathogen Host Defence Hypothesis (PATHOS-D) – suggests that depression reflects a phenotypic suite of behavioural and physiological responses evolved to mitigate mortality risk linked to pathogens (Raison and Miller, 2013). Psychosocial stress is argued to have been predictive of wounding and subsequent infection in ancestral environments – where low social support and isolation is supposed to have increased attacks from predatory species or conspecifics – driving selection for a pre-emptive response. The bargaining hypothesis, along with the related psychic pain hypothesis (Hagen and Barrett, 2007), and arguments proposing PND evolved as a distress signal to elicit support (Crouch, 1999; Crouch, 2002), in particular from kin and the infant's father (Rantala et al., 2018), would all anticipate increased rates of PND in the childrearing conditions created by the pandemic. The PATHOS-D would also predict elevated rates of PND resulting from psychosocial stress associated with lockdown. We do not consider our data to favour any one hypothesis in particular; current hypotheses regarding the evolution of PND and depression more generally are also not without their critics (Nettle, 2004; Myers et al., 2016, 2017; Rantala et al., 2018). Nonetheless, regardless of the evolutionary origins, postnatal depressive symptoms are undoubtedly an indicator of distress and if relatives were most likely to come to a mother's aid, inclusive fitness would explain why. Needs-based kin altruism in the context of reproduction and childrearing has been reported elsewhere (Schaffnit and Sear, 2017; Page et al., 2019a,b), and our findings may suggest that a limited number of family members "took the risk" to provide practical support for mothers.

New mothers are obviously not the only people to experience significant reductions in their social contact, posing the question as to whether the findings here simply reflect a population-wide elevation in depressive symptomology; or do postnatal women constitute a specific risk group during the ongoing pandemic. We suggest the answer to both these questions is "yes." There is a mounting body of work supporting the contention that the prevalence of depression symptoms has increased at the population level (Bueno-Notivol et al., 2021); for example, a survey of the general adult population in the United States found a three-fold increase compared to pre-pandemic levels (Ettman et al., 2020) and childhood depression data from the United Kingdom also suggests symptom elevation (Bignardi et al., 2020). However, evidence from the United Kingdom suggests that after an initial increase in symptoms in the run up to lockdown (Shevlin et al., 2020), depressive symptoms in the adult population declined from an elevated starting point across the first 20 weeks of lockdown, suggesting people adjusted (Fancourt et al., 2020). While our data cannot speak to other groups, given social support and social isolation are negatively associated with depressive symptoms across age groups in the general population in Western contexts (Lakey and Cronin, 2008; Gariépy et al., 2016), it seems reasonable to suggest that lessons from our quantitative findings may generalise beyond postnatal mothers. It is also clear that the impact of the COVID-19 pandemic is

not equitable and there is widespread evidence that structural inequalities along such lines as socioeconomic position, race, and gender are creating differential burdens. We would encourage future studies examining the role of social networks in shaping depressive experience during the pandemic across other groups, to identify those most at risk and possible intervention strategies.

In the United Kingdom, cultural norms of intensive mothering arguably slowed down policy shifts to allow childcare support during periods of lockdown (Emmott et al., 2021), and there have been many reports of partners and other key supporters being prohibited from antenatal appointments and births, financial support packages have been geared toward the male workforce, and there has been widespread rhetoric from politicians and the popular press encouraging the gendered division of childcare responsibilities, all to the detriment of mothers (Emmott et al., 2021). Add to this parenting stresses which are arguably more common in the postnatal period – for instance, sleep deprivation, postpartum pain, the need to learn/relearn skills such as breastfeeding – and it appears reasonable to suggest that postnatal mothers are at particularly high risk of depression during the ongoing pandemic. However, there are at least two studies reporting a *decrease* in postnatal depressive risk during the pandemic; southern Israeli women giving birth in quarantine showed lower PND prevalence (Pariente et al., 2020), as did mothers of lower socioeconomic status (SES) in New York (Silverman et al., 2020). Rather than casting doubt on our findings, these studies highlight the contextually specific impact of social distancing measures; the authors of the Israeli study speculate that the mothers in their sample benefited from greater family support in this context (Pariente et al., 2020), while lower SES mothers in New York appear to have benefited from both not having to work themselves and increased childcare support from partners forced to stay at home (Silverman et al., 2020). These studies align with the finding from our qualitative results that some women experienced greater support from working-from-home partners than they might otherwise have done. Scelza and Hinde (2019) have recently argued that human evolution took place in "an adaptive sociocultural perinatal complex" typified by extensive social support for the mother-infant dyad, resulting from the energetic and physical demands of gestation, birth, breastfeeding, and the dependent state in which infants are born and the slow rates at which they develop. To protect maternal mental health, evidence suggests we should protect this perinatal complex, both during the ongoing COVID-19 pandemic and beyond.

Limitations

Convenience sampling, predominantly recruiting via social media, leads to potential biases, particularly in relation to the degree to which our sample's use of online technology for communication and support seeking is representative. Our participants were relatively homogenous in terms of ethnicity and family formation; thus, the extent to which these findings generalise to other mothers from London, the United Kingdom, and other high-income contexts is unknown. Further, the median wage in London in 2019 was £38,272 (Office for National Statistics, 2019), putting a two-person household at approximately £76.5K; only 34% of our sample had a household income before tax of between £0–75K. Low SES is a known risk factor for PND, and lower SES has been found to increase the risk of depression among adults in the United States during the pandemic; thus it is possible the rate depressive symptoms based on our sample were an underestimate of the actual rates in London (although see Silverman, et al., 2020).

Specifically relating to our quantitative study, the sample size of women giving birth during lockdown was small (n = 47), limiting the confidence in any apparent differences between maternal experience dependent on timing of birth before and during lockdown. Beyond the findings regarding communication with social network members, the confidence intervals for all other measures in our models are wide and overlap one, which is suggestive of a lack of statistical power. Maternal social networks were measured by asking participants to list "important people"; however, our qualitative results suggest contact with peers who are not necessarily important at an individual level may be a key aspect of maternal social networks, which we are unable to quantitatively test in our data. Our models captured only limited variance in depressive symptoms, suggesting unaccounted for factors were playing an important role in maternal wellbeing, which is unsurprising. Two important factors, known to be predictive of PND risk, which our models cannot speak to are a mother's level of access to social support (Fellmeth et al., 2021) – both in terms of received and perceived practical and emotional support – and previous history of mental health issues (Spry et al., 2021); for a comprehensive review of other PND risk factors see Yim et al. (2015). We also have no data on whether participants had sought or were currently receiving medical attention for PND. Finally, the cross-sectional nature of our data means inferences of the direction of causation between communication and depressive symptoms are untestable; we also do not know the timing of any symptom onset or prior history of depression, which would help speak to the direction of causation.

In terms of our qualitative study, the relatively brief nature of open-text responses means that our findings are unlikely to capture the full range and nuance of maternal experiences during lockdown. Due to the open nature of the survey questions and the brevity of responses, our findings provide descriptions of various maternal experiences at sample-level. It is therefore unclear how wide-ranging these experiences were, and if or how these themes overlapped at an individual level.

CONCLUSION

To paraphrase another study of maternal mental health during the COVID-19 pandemic (Davenport et al., 2020), mothers in London were not OK during England's first lockdown, with a substantial number of women meeting the diagnostic criteria for PND. While Western childrearing norms focus on intensive parenting (Faircloth, 2014), our results highlight that it still "takes a village" to raise children in high-income populations. Several studies from Europe and the United States have found that maternal domestic work and childcare increased during the COVID-19 pandemic (Calarco et al., 2020;

Del Boca et al., 2020; Prados and Zamarro, 2020; Zoch et al., 2020), suggesting that the burden of lockdown may have disproportionately impacted mothers. While our qualitative results suggest high partner involvement may have been associated with more positive experiences of lockdown, and a Canadian study found lockdown may have encouraged greater partner participation in domestic work and caregiving (Shafer et al., 2020), overall, our results indicate that adequate support within the household was either not available or not enough for many mothers in our sample.

As cooperative childrearers, the availability of extended support from beyond the nuclear family is crucial, and in our study mothers with communication with larger social networks during lockdown fared better in terms of maternal mental health. Since the time of our data collection, mothers in London have experienced two further periods of lockdown – one for approximately a month over November 2020 and the second, beginning on December 20th and only beginning to ease at the time of writing. Recognising the vulnerability of new parents, from the 2nd December, households in England with infants were allowed to form a "support bubble" and have in-person contact with one other household (Department of Health and Social Care, 2020), which may help alleviate the detrimental impact of lockdown on maternal mental health. However, in-person contact comes with infection risk, and we anticipate face-to-face contact across maternal social networks will remain low due to ongoing restrictions. Previous studies have found that online social contact is a valued source of social support for mothers (Archer and Kao, 2018; Price et al., 2018; Teaford et al., 2019). Remote communication could potentially be a solution, with our findings of lower depressive symptoms among mothers who had remote communication with a higher proportion of their personal network that they had not also seen in person. However, our qualitative findings suggest that seeking support and information may be more challenging via remote communication – several studies have also highlighted the costs of remote communication, including "Zoom fatigue" (Archer and Kao, 2018; Epstein, 2020). It is important, therefore, that the burden of seeking contact does not fall on the mother. Instead, encouraging people to virtually reach out to the mothers that they know may be a low-risk way of improving maternal mental health in high-income contexts, where most people have the means to do so.

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 the UCL Research Ethics Committee. The participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

SM led the project, designed and managed the data collection, cleaned the data, and conducted the quantitative analysis. EE supported the data collection and conducted the qualitative analysis. SM and EE interpreted the quantitative and qualitative results, and wrote the manuscript. Both authors contributed to the article and approved the submitted version.

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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.2021.648002/full#supplementary-material. The legends for the Supplementary Figures can be found in **Supplementary Material 1**.

Table 1.docx – 'Supplementary Material 1'

Table 2.xlsx – 'Supplementary Material 2'

Image 1.TIFF – 'Supplementary Figure 1'

Image 2.TIFF – 'Supplementary Figure 2'

Image 3.TIFF – 'Supplementary Figure 3'

Image 4.TIFF – 'Supplementary Figure 4'

Image 5.TIFF – 'Supplementary Figure 5'

Image 6.TIFF – 'Supplementary Figure 6'

Image 7.TIFF – 'Supplementary Figure 7'

Image 8.TIFF – 'Supplementary Figure 8'

Image 9.TIFF – 'Supplementary Figure 9'

Image 10.TIFF – 'Supplementary Figure 10'

Image 11.TIFF – 'Supplementary Figure 11'

Image 12.TIFF – 'Supplementary Figure 12'

Image 13.TIFF – 'Supplementary Figure 13'

Image 14.TIFF – 'Supplementary Figure 14'

Image 15.TIFF – 'Supplementary Figure 15'

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BRIEF RESEARCH REPORT
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Testing the Disgust-Based Mechanism of Homonegative Attitudes in the Context of the COVID-19 Pandemic

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Negative attitudes and stigmatization can originate from the perception of a disease-related threat. Following the spread of the COVID-19 pandemic, it is often suggested that incidents of discriminatory behavior are the result of defense mechanisms aimed at avoiding pathogens. According to the behavioral immune system theory, people are motivated to distance themselves from individuals who show signs of infection, or who are only heuristically associated with a disease, primarily because of the disgust they evoke. In this paper we focus on negative attitudes toward gay men and lesbians who are among social groups that have been persistently framed as "unclean." In our correlational study (N = 500 heterosexual participants; Polish sample data collected during the first COVID-19 lockdown in Poland, in March/April 2020) we tested moderation models derived from the behavioral immune system theory. Specifically, we investigated whether perceived vulnerability to disease and perceived threat of contracting COVID-19 moderate the relation between disgust and homonegativity. We found that sexual disgust (but not pathogen nor moral disgust) predicted homonegative attitudes. This effect was stronger for participants expressing higher levels of perceived vulnerability to disease but was not dependent on the perception of the COVID-19 threat. The results reaffirm previous evidence indicating a pivotal role of disgust in disease-avoidance mechanisms. They also point to functional flexibility of the behavioral immune system by demonstrating the moderating role of perceived vulnerability to disease in shaping homonegative attitudes. Finally, they show that the threat of COVID-19 does not strengthen the relationship between disgust and homonegativity.

Keywords: behavioral immune system, disgust, homonegativity, gay, lesbian, COVID-19

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INTRODUCTION

The COVID-19 pandemic has set the ground for testing disease-related mechanisms of various social phenomena in real pathogen-threat conditions. In this context, one of the highly relevant domains concerns social attitudes, as they often have disease-related origins (Faulkner et al., 2004). Here, we focus on homosexual individuals, both men and women, who have been frequently framed as "unclean," and associated with germs and diseases (such as AIDS) (Crandall et al., 1997; Herek, 2002; Greene and Banerjee, 2006; Golec de Zavala et al., 2014; Pachankis et al., 2015; Filip-Crawford and Neuberg, 2016).

One of the most relevant theoretical frameworks applied to explain negative social attitudes such as prejudice, ethnocentrism, or homonegativity, is the evolution-based theory of the behavioral immune system (BIS; Curtis et al., 2011; Murray and Schaller, 2016; Ackerman et al., 2018). As mobilizing the physiological immune system is metabolically costly (Conner and Grisham, 1996), it was suggested that another set of psychological defense mechanisms designed to mitigate the threat of disease before infection occurs should have evolved (Schaller and Park, 2011). Indeed, the behavioral immune system operates by changing cognition, affect, and behavior in ways that promote pathogen avoidance (Ackerman et al., 2018). The initial detection of threat-relevant cues in the environment triggers affective reactions, leading to adaptive behavior. However, as distinct cues imply different risks, behavioral immune system exhibits functional flexibility to both individual (e.g., perceived self-infectability) and contextual (e.g., a pandemic) factors (Ackerman et al., 2018). For instance, temporarily heightened vulnerability to disease amplifies negative reactions to foreigners, particularly of nationalities less familiar to the participants (Faulkner et al., 2004). Additionally, vaccinated participants tend to express less prejudice toward immigrants than do unvaccinated participants (Huang et al., 2011). The BIS is also prone to overgeneralization. Similarly to a smoke detector, it sometimes becomes activated even in the absence of a real disease threat. Thus, we can observe avoidance tendencies triggered by the presence of non-infectious physical and mental abnormalities, such as disfigurements, disabilities, or obesity (Park et al., 2003; see also Nussinson et al., 2018).

Researchers point to disgust as the fundamental affective factor underlying pathogen avoidance mechanisms, because it functions as the first line of defense against infection (see Oaten et al., 2009, for a review). Disgust triggers reactions directed to minimize disease risk after we have encountered the disease threat, motivating us to avoid contaminated sources before we come into contact with them (Rubio-Godoy et al., 2007). To date, there is a large body of empirical data demonstrating the crucial role of disgust and disgust sensitivity in shaping social attitudes and behaviors. Disgust facilitates out-group dehumanization (Buckels and Trapnell, 2013) and xenophobia (Zakrzewska et al., 2019), as well as prejudicial reactions to individuals not being actually diseased but only heuristically associated with the presence of diseases (e.g., obese or disfigured people; Harvey et al., 2002). It has recently been suggested that the behavioral immune system uses out-group membership as a cue for infectiousness (Bressan, 2020).

Nussbaum (2001) claimed that homosexuality frequently appears as an object of disgust. Indeed, a substantial body of research points to the relationship between disgust and homonegative attitudes (Herek, 1993). For instance, manipulating disgust by exposing participants to a noxious ambient odor amplifies negative attitudes toward sexual minorities (Inbar et al., 2012). Additionally, Inbar et al. (2009) demonstrated that individuals high in disgust sensitivity perceived gay people more negatively than did those low in disgust sensitivity. What seems to be the crucial point is that the observed impact of disgust on attitudes tends to be larger in response to gay men than lesbians (Inbar et al., 2012; Kiss et al., 2020). The reason for that could be that gay men's engagement in anal intercourse is perceived as unhygienic (Kiss et al., 2020) and that male homosexuality is associated with germs and diseases such as AIDS (Crandall et al., 1997; Pachankis et al., 2015). Bettinsoli et al. (2019) showed that across 23 countries, gay men were disliked more than lesbians. Therefore, it is strongly recommended to analyze data on attitudes toward gay men and lesbians separately (Kiss et al., 2020).

Another key issue relates to the multifaceted nature of disgust. Despite the common ground in the form of the affective state of repulsion, different facets of disgust (i.e., pathogen, moral, and sexual) are considered to be designed by natural selection to solve different functional problems (Tybur et al., 2009). Pathogen disgust motivates the avoidance of diseases and is likely to be elicited when a pathogenic threat is salient. Sexual disgust motivates the avoidance of sexual partners and behaviors that can lead to negative biological repercussions (e.g., sex with genetic relatives). However, it has also been suggested that sexual stimuli and behaviors that transgress culturally normative conceptualizations of sexuality may trigger sexual disgust (Morrison et al., 2019). Likewise, it should be indicated that perceived vulnerability to disease (PVD; Duncan et al., 2009) correlates positively with pathogen disgust and sexual disgust (Tybur et al., 2009). This is understandable, as there are substantial disease risks associated with sexual behavior. Moral disgust, the final domain of disgust, drives the avoidance of social norm violators and is distinct from the other two domains (Tybur et al., 2009).

The evidence identifying the relationship between specific disgust domains and homonegativity is highly inconsistent. The vast majority of studies demonstrating that disgust sensitivity predicts an increased level of homonegative attitudes focused primarily on only one domain of this phenomenon, namely, pathogen disgust (Haidt et al., 1994; Inbar et al., 2009, 2012). Some studies that relied on the more sophisticated scale of three domains of disgust (TDDS; Tybur et al., 2009) showed stronger associations between homonegative attitudes and sexual disgust than pathogen or moral disgust (Ray and Parkhill, 2020). However, some research indicated that there are no associations at all (Smith, 2012). Specifically, Smith (2012) manipulated pathogen and moral disgust (but not sexual disgust) and found no causal relationship between these two disgust types, and implicit and explicit anti-gay attitudes. Taking all these insights into account, it seems that it is still an open question as to which type of disgust, if any, is the most prominent predictor of homonegativity (see also Smith, 2012; Ray and Parkhill, 2020).

Our study focused on three domains of disgust as potential predictors of homonegative attitudes in the context of the COVID-19 pandemic. On the basis of the BIS theory, we hypothesized that pathogen and sexual disgust would predict negative attitudes toward gay persons, and that this effect would be stronger for gay men than for lesbians. It could be argued that sexual disgust is not directly related to pathogen threats and, as such, cannot be derived from the theory of BIS as a predictor of social attitudes (Ray and Parkhill, 2020). We want to make a different argument that, since certain pathogens

can be transmitted sexually (e.g., through anal intercourse), sexual disgust becomes an important indicator of BIS activation. Thus, we expect sexual disgust to be a stronger predictor of homonegative attitudes than pathogen disgust.

Moreover, we predict that the above effects will be moderated by concerns about disease. As the assumptions of BIS theory (e.g., Schaller and Park, 2011) and previous research suggest, worrying about contracting an illness can significantly predict social attitudes (such as prejudice). This anxiety can have various origins—it can result from individual differences (e.g., perceiving one's vulnerability to disease) and can also depend on external circumstances (e.g., temporarily activated salience of pathogens). Thus, we predict that perceived vulnerability to disease will moderate the effect. Specifically, we predict that individuals who express higher levels of PVD will show a stronger connection between disgust and homonegativity than those expressing lower levels of this variable. Furthermore, we wanted to investigate whether the relation between disgust and homonegativity is moderated by the perceived threat of contracting COVID-19. As Faulkner et al. (2004) noticed, any contextual information that implies increased vulnerability to infection may amplify negative reactions to categories of people heuristically associated with a disease. What follows is that a specific psychological reaction (such as disgust or perceived vulnerability to illness) may be associated with the perceived threat of disease in a given situation. Indeed, a temporary salience of disease amplifies xenophobic attitudes (Faulkner et al., 2004), similarly to disease salience decreasing the desire to affiliate with out-group members (Millar et al., 2020). Importantly, it has been shown that activating COVID-19 concerns (by reading about mortality statistics and government lifestyle regulations) results in higher germ aversion among participants, compared to the control condition (Bacon and Corr, 2020). Stevenson et al. (2021) also indicated that students showed higher levels of core disgust and germ aversion during the COVID-19 lockdown in Australia than before the COVID-19 pandemic. Similarly, Polish women reported higher levels of disgust sensitivity during the COVID-19 pandemic than during the pre-pandemic period (Miłkowska et al., 2021). In addition, Shook et al. (2020) showed that those who were higher in germ aversion and pathogen disgust sensitivity were more concerned with COVID-19 and expressed more preventative behaviors. On the other hand, recent reports indicating the increase of prejudice against Chinese individuals (for more details see: Ackerman et al., 2021), or attacks against the LGBT community in Poland[1] should also be addressed. It is suggested that these negative reactions may be heightened by the pandemic, which may be interpreted as evidence supporting the BIS theory. However, this may not necessarily be the case. What should be highlighted here is that a pandemic is not a type of event that occurs frequently over a course of a human lifetime. Historically it has also been a rare phenomenon, due to multiple features of ancestral societies, such as relatively small-scale geographic mobility and limited routes of disease transmissions. For this reason, it is unlikely that defense mechanisms specific to pandemics have evolved among humans (Ackerman et al., 2021; see also Varella et al., 2021).

Taking these considerations into account, we investigated whether the threat of COVID-19 plays any significance in moderating the BIS mechanism. Specifically, we tested whether a higher level of the perceived threat of COVID-19 would be associated with a stronger relation between disgust sensitivity and homonegativity.

MATERIALS AND METHODS

Participants

We recruited Polish respondents from the SWPS University of Social Sciences and Humanities (through the Sona system) and a social media web page[2]. The final sample consisted of 588 participants who agreed to participate in the study on social attitudes and complete a web-based survey through Qualtrics. We conducted a frequency analysis, which revealed that 60 participants reported being bisexual, 24 reported being gay, and 4 participants chose the "other" option regarding their sexual orientation. For this study, we analyzed data for participants who identified as heterosexual: 500 respondents (421 women and 79 men; M_{age} = 20.18, SD = 9.20). Sensitivity calculations made using the G*Power 3.1.9.2 software (Faul et al., 2007) indicate that for a model including one tested predictor and three total predictors, the N = 500 sample is sufficient to detect an effect at a size of $f > 0.016$ ($R^2 > 0.0157$) with 1-Beta > 0.8. Given that the observed R^2 for all significant moderations is > 0.2, our study has sufficient power. Data collection started on March 18, 2020, after the government announced the first COVID-19 pandemic lockdown in Poland, and ended on April 9, 2020.

Procedure and Materials

Disgust Propensity

To measure disgust propensity, we used the Three Domains of Disgust Scale (TDDS; Tybur et al., 2009). The questionnaire describes 21 situations that refer to three disgust domains: *pathogen disgust* (e.g., "Standing close to a person who has body odor"), *sexual disgust* (e.g., "Performing oral sex"), and *moral disgust* (e.g., "Students cheating to get good grades"). Participants used a 7-point scale (from 1 = *it is not disgusting at all* to 7 = *it is extremely disgusting*) to rate each situation. We averaged scores for the three subscales separately: moral disgust (α = 0.81), pathogen disgust (α = 0.70), and sexual disgust (α = 0.76).

Homonegativity

We used the Modern Homonegativity Scale (MHS; Morrison and Morrison, 2002) to separately measure attitudes toward gay men (MHS-G; α = 0.92) and lesbians (MHS-L; α = 0.93). Each scale consists of 12 statements that participants rated from 1 = *strongly agree* to 5 = *strongly disagree*. We also created a general index of homonegativity by averaging the results about lesbians and gay men (MHS; α = 0.97).

[1] https://www.reuters.com/article/us-poland-lgbt-europe-trfn-idUSKBN2AA20S

[2] www.facebook.pl

Perceived Vulnerability to Disease

To measure subjective perceptions of susceptibility to disease, we used the PVD scale (Duncan et al., 2009). The scale is composed of two subscales: perceived infectability (PI; 7 items; $\alpha = 0.80$) and germ aversion (GA; 8 items; $\alpha = 0.71$). The perceived infectability subscale refers to one's beliefs about their susceptibility to infectious diseases. In comparison, the germ aversion subscale assesses emotional discomfort in contexts involving a high risk of pathogen transmission. The scale consists of 15 statements rated by respondents on a 7-point scale (from 1 = *strongly disagree* to 7 = *strongly agree*). Some researchers investigating the role of perceived vulnerability to disease analyzed the general index of PVD (Faulkner et al., 2004), while others analyzed the subscales separately (Smith, 2012; Brown and Sacco, 2020). As the subscales emphasize different aspects of perceived vulnerability (germ aversion is more emotion-based, while perceived infectability is more cognitive-based), we decided to investigate the role of GA and PI separately.

Perceived Threat of COVID-19

To measure the perceived threat of COVID-19, participants indicated their agreement with eight statements on a 7-point scale (from 1 = *strongly disagree* to 7 = *strongly agree*). The scale included items measuring the extent to which participants perceived coronavirus to be a threat to their lives (e.g., "I think that coronavirus is a real threat to my life" and "I am convinced that the media are exaggerating the threat of coronavirus"). Ratings for these items were averaged to form an index of the perceived threat of COVID-19 ($\alpha = 0.71$)[3].

RESULTS

We first calculated descriptive statistics for all variables and examined Pearson's correlations between all variables using IBM SPSS Statistics 25. We adjusted threshold levels of significance for correlation coefficients due to Bonferroni correction. In the next step, we conducted multiple moderation analyses using Model 1 PROCESS (Hayes, 2013).

Initial Analyses

Descriptive statistics and correlation coefficients between continuous variables are presented in **Table 1**. To maintain the type I error rate at approximately 5% and reduce the probability of this error occurring in multiple testing, we decided to use Bonferroni correction to adjust the level of statistical significance of correlation coefficients (Curtin and Schulz, 1998). For this purpose, we divided the critical level of significance (0.05) by the number of tests performed (36), which resulted in an adjusted level of significance $\alpha = 0.001$. We found that pathogen disgust positively correlated with sexual disgust ($r = 0.28$, $p < 0.001$) but not with moral disgust ($r = 0.14$, $p = 0.002$). Pathogen disgust was positively correlated with GA ($r = 0.38$, $p < 0.001$) but not with PI ($r = 0.11$, $p = 0.011$), and positively correlated with the perceived threat of COVID-19 ($r = 0.18$, $p < 0.001$). Sexual disgust positively correlated with GA ($r = 0.21$, $p < 0.001$) and with homonegativity toward gays ($r = 0.28$, $p < 0.001$), lesbians ($r = 0.28$, $p < 0.001$), and general homonegativity ($r = 0.28$, $p < 0.001$). The perceived threat of COVID-19 positively correlated with PI ($r = 0.56$, $p < 0.001$) and with GA ($r = 0.32$, $p < 0.001$). Two dimensions of PVD were positively correlated ($r = 0.28$, $p < 0.001$), as were homonegativity indexes toward gays and lesbians ($r = 0.94$, $p < 0.001$).

Moderation Analyses: PVD as a Moderator

First, we tested whether the two subscales of the PVD scale (PI and GA) moderated the positive relation between disgust sensitivity and negative attitudes separately toward gay men and lesbians. As the only domain of disgust that significantly predicted homonegativity was sexual disgust, we present all the analyses exclusively for that kind of disgust. The results of analyses conducted for pathogen and moral disgust are presented in **Supplementary Tables 1–4**. All moderation analyses were conducted using Model 1 PROCESS (Hayes, 2013) with sex, education, and age as controlled variables[4]. We calculated age

[3]We also had additional measures in the study (political beliefs, self-perceived religiosity, subjective well-being, agreement with the government's decisions regarding COVID-19, sense of control, system justification, social distancing toward out-groups, pregnancy, gestational age, fertility, last flu vaccination, education level, and earnings). We do not discuss them, as they served to verify hypotheses not related to the topic presented here.

[4]These variables should be controlled if not taken into consideration (see for example Oaten et al., 2009; Ackerman et al., 2018). We provide the description of the effects of covariates in **Supplementary Material**.

TABLE 1 | Means, standard deviations, and correlations among study variables ($N = 500$).

Variables	*M*	*SD*	1	2	3	4	5	6	7	8	9
1. Pathogen disgust	5.21	0.84	–								
2. Sexual disgust	3.54	1.08	0.28*	–							
3. Moral disgust	5.22	0.96	0.14	0.13	–						
4. Perceived threat of COVID-19	4.12	0.86	0.18*	0.19	0.04	–					
5. Perceived infectability	3.79	1.04	0.11	0.01*	0.02	0.56*	–				
6. Germ aversion	4.46	0.99	0.38*	0.21*	–0.01	0.32*	0.28*	–			
7. MHS-gays	2.79	0.83	0.02	0.28*	0.06	–0.13	–0.14	0.05	–		
8. MHS-lesbians	2.77	0.84	0.05	0.28*	0.07	–0.12	–0.13	0.05	0.94*	–	
9. General homonegativity (MHS)	2.78	0.82	0.03	0.28*	0.07	–0.13	–0.14	0.05	0.99*	0.99*	–

*Cell entries are zero-order Pearson correlation coefficients adjusted due to Bonferroni correction of the p-value, *p < 0.001.*

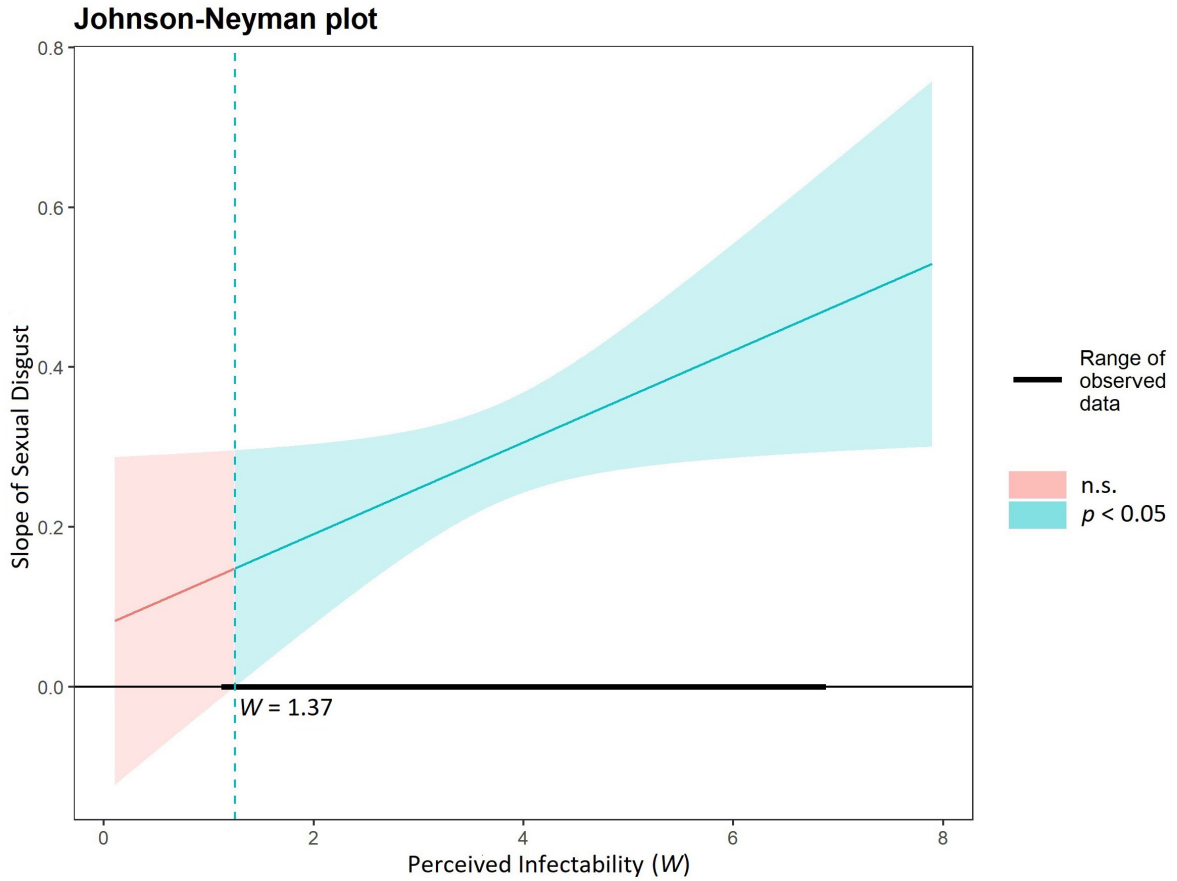

FIGURE 1 | Regions of significance for the conditional effect of sexual disgust presented for perceived infectability as a moderator and negativity toward gay men as the outcome variable.

as a continuous variable and education as a 3-categorical ordinal variable: primary, secondary, and higher education.

The Moderating Role of Perceived Infectability in the Relationship Between Sexual Disgust and Negative Attitudes Toward Gay Men

In the first analysis, we introduced sexual disgust as a predictor, negative attitudes toward gay men as the outcome variable, and PI as the moderating variable. The model was significant, $F_{(6,489)} = 24.60$, $p < 0.001$, $R^2 = 0.23$, just as the expected moderation was: $b = 0.06$; 95% $CI = [0.008, 0.114]$. We probed this interaction by using the Johnson-Neyman technique (Hayes and Matthes, 2009), which allowed us to identify the regions of significance for the conditional effect of sexual disgust. As shown in **Figure 1**, when PI was lower than 1.37, the predicted relation between sexual disgust and negative attitudes toward gay men was not salient. However, starting from the 1.37 point, the higher the PI level, the stronger the relation between sexual disgust and homonegativity toward gay men, which is consistent with our hypotheses. The simple slopes analysis revealed that low, moderate, and high values of PI positively predicted attitudes toward gay men: the coefficient on 1 *SD* below the mean was 2.73, $b = 0.22$; 95% $CI = [0.141, 0.305]$, on the mean was 3.77, $b = 0.29$; 95% $CI = [0.226, 0.348]$, and on 1 *SD* above the mean was 4.81, $b = 0.35$; 95% $CI = [0.268, 0.432]$. Detailed results are presented in **Supplementary Table 5**.

The Moderating Role of Perceived Infectability in the Relationship Between Sexual Disgust and Negative Attitudes Toward Lesbians

The complementary analysis for negative attitudes toward lesbians as the outcome variable, sexual disgust as a predictor, and PI as the moderating variable, revealed that the model was significant, $F_{(6,489)} = 23.42$, $p < 0.001$, $R^2 = 0.22$, as was the moderation effect, $b = 0.06$; 95% $CI = [0.003, 0.110]$. As we present in **Figure 2**, when PI was lower than 1.25, there was no predicted relationship between sexual disgust and negative attitudes toward lesbians. Starting from 1.25 points, the higher the PI level, the stronger the relationship between sexual disgust and negative attitudes toward lesbians. The simple slopes analysis revealed that low, moderate, and high values of PI positively predicted negative attitudes toward lesbians: the coefficient 1 *SD* below the mean was 2.73, $b = 0.23$; 95% $CI = [0.150, 0.317]$, at the mean was 3.77, $b = 0.29$; 95% $CI = [0.230, 0.354]$, and 1 *SD* above the mean was 4.81, $b = 0.35$; 95% $CI = [0.268, 0.435]$. Detailed results are presented in **Supplementary Table 6**.

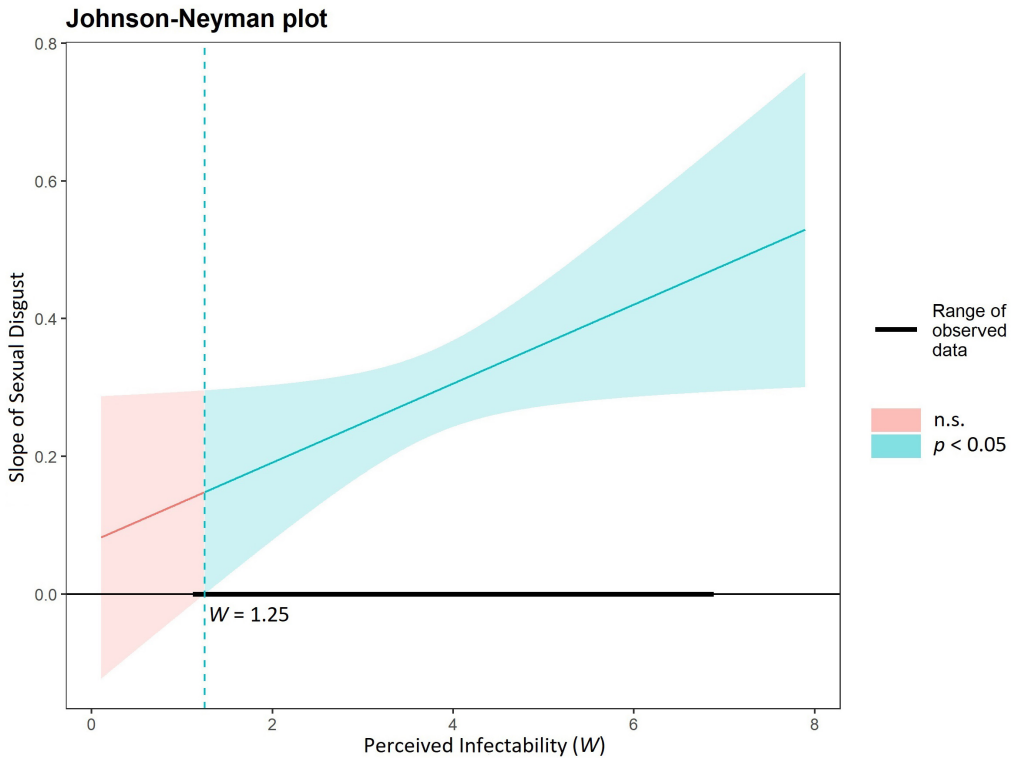

FIGURE 2 | Regions of significance for the conditional effect of sexual disgust presented for perceived infectability as a moderator and negativity toward lesbians as the outcome variable.

The Moderating Role of Germ Aversion in the Relationship Between Sexual Disgust and Negative Attitudes Toward Gay Men

To test the other facet of PVD, we introduced GA as the moderating variable, sexual disgust as a predictor, and negative attitudes toward gay men as the outcome variable. The model was significant, $F_{(6,489)} = 21.53$, $p < 0.001$, $R^2 = 0.21$, but we found no moderation effect, $b = 0.04$; 95% CI = [-0.021, 0.094]. Detailed results are presented in **Supplementary Table 5**.

The Moderating Role of Germ Aversion in the Relationship Between Sexual Disgust and Negative Attitudes Toward Lesbians

We provided the complementary analysis for negative attitudes toward lesbians as the outcome variable, sexual disgust as a predictor, and GA as a moderator. The model was significant, $F_{(6,489)} = 20.73$, $p < 0.001$, $R^2 = 0.20$; however, we found no moderation effect, $b = 0.03$; 95% CI = [-0.025, 0.092]. Detailed results are presented in **Supplementary Table 6**.

Moderation Analyses: The Perceived Threat of COVID-19 as a Moderator

The next set of moderation analyses introduced the perceived threat of COVID-19 as the moderator in the relationship between sexual disgust and homonegativity. Again, all presented moderation analyses were conducted using Model 1 PROCESS (Hayes, 2013) with sex, education, and age as controlled variables.

The Moderating Role of the Perceived Threat of COVID-19 in the Relationship Between Sexual Disgust and Negative Attitudes Toward Gay Men

We conducted this analysis using sexual disgust as a predictor, attitudes toward gay men as the outcome variable, and perceived threat of COVID-19 as a moderator. The model was significant, $F_{(6,577)} = 21.41$, $p < 0.001$, $R^2 = 0.18$; however, we found no moderation effect, $b = 0.04$; 95% CI = [-0.019, 0.102]. Detailed results are presented in **Supplementary Table 5**.

The Moderating Role of the Perceived Threat of COVID-19 in the Relationship Between Sexual Disgust and Negative Attitudes Toward Lesbians

The complementary analysis was conducted for lesbians with homonegativity as the outcome variable, sexual disgust as a predictor, and perceived threat of COVID-19 as a moderator. The model was significant, $F_{(6,577)} = 20.35$, $p < 0.001$, $R^2 = 0.18$, but again, we found no moderation effect, $b = 0.04$; 95% CI = [-0.017, 0.106]. Detailed results are presented in **Supplementary Table 6**.

DISCUSSION

Disease avoidance mechanisms and their potential role in explaining social attitudes have recently received much scientific attention (e.g., Mentser and Nussinson, 2020; Kramer and Bressan, 2021). In the context of the ongoing COVID-19 pandemic, they have become even more pertinent (Bressan, 2020;

Seitz et al., 2020; Hromatko et al., 2021). Our study was designed to test the predictions emerging from the behavioral immune system theory (Ackerman et al., 2018). Specifically, we tested whether pathogen and sexual (but not moral) disgust would predict negative attitudes toward gay men and lesbians, and whether perceived vulnerability to disease (i.e., perceived infectability, germ aversion) and perceived threat of COVID-19 moderated these predicted associations.

Our results point to the significance of sexual disgust in predicting homonegative attitudes. The more participants declared experiencing sexual disgust, the more negative attitudes they held toward gay men and lesbians. Surprisingly, we did not notice any effects to be stronger for gay men than lesbians. Additionally, along with our hypotheses, moral disgust did not play any role in predicting homonegative attitudes. However, contrary to our expectations, pathogen disgust did not predict homonegativity either. Although we predicted that the relationship between pathogen disgust and homonegativity would not be as strong as in the case of sexual disgust, pathogen disgust produced no effects at all. Such results resonate with the data demonstrated by Smith (2012), and Ray and Parkhill (2020).

Ray and Parkhill (2020) showed that the relationship between heteronormativity and hostility toward gay men was mediated by sexual disgust but not pathogen or moral disgust. Importantly, they argued that the null effects for pathogen disgust eliminate the disease-avoidant approaches (i.e., BIS) as reasonable frameworks for explaining hostility toward gay men. In our view, such a conclusion would be warranted only if we could be absolutely certain that sexual disgust is not associated with pathogen avoidance. However, although pathogen disgust and sexual disgust proved their undeniable distinctiveness, they also showed some similarities in terms of pathogen avoidance (Tybur et al., 2009). Specifically, both pathogen and sexual disgust showed positive and equally strong relationships with PVD, indicating that each of them can motivate disease-avoidant behaviors. This was predicted by the authors of TDDS (Tybur et al., 2009), who considered the potential disease risk associated with sex. Taking these findings into account, our results would suggest that sexual disgust is the most likely determinant of homonegative attitudes, however it may also carry a disease-avoidant function. This points to the specificity of the disgust-driven mechanisms. As gay persons can be viewed in light of their sexual behavior and associated with sexually transmitted diseases (Pachankis et al., 2015), it is primarily sexual disgust that may prominently drive attitudes toward them, rather than pathogen disgust.

Our data partly confirmed the moderating role of perceived vulnerability to disease in the relationship between sexual disgust and negative attitudes toward gay men and lesbians. We observed the expected effects for the perceived infectability subscale but not for the germ aversion subscale of PVD. Specifically, the more participants perceived themselves as susceptible to diseases, the stronger was the association between sexual disgust and negative attitudes for both gay men and lesbians. This supports the idea of the behavioral immune system and its flexibility: the system's response differs depending on the individual's perceived vulnerability to disease (Ackerman et al., 2018). However, it is unclear why the results were significant only for the cognition-based facet of the PVD, and not for the germ aversion subscale. Perhaps, just as in the case of pathogen disgust measured by TDDS, the items of the GA subscale do not cover aversion toward sexually transmitted pathogens (examples of items: "It truly bothers me when people sneeze without covering their mouths," "I do not like to write with a pencil someone else has obviously chewed on," "I prefer to wash my hands pretty soon after shaking someone's hand"). On the other hand, the PI subscale refers to a rather general vulnerability to wide classes of diseases.

Analyses for the moderating role of the perceived threat of COVID-19 showed that this kind of threat played no role in the relationship between sexual disgust and homonegativity. Situational circumstances, such as a pandemic, are thought to strengthen the potential effects of disease-avoidance mechanisms (e.g., Bacon and Corr, 2020; Millar et al., 2020; Sorokowski et al., 2020; Hromatko et al., 2021; Miłkowska et al., 2021; Stevenson et al., 2021). Our research indicates, however, that concerns about COVID-19 have no effect on attitudes toward gay persons. The perceived likelihood of becoming infected with this illness did not strengthen the relationship between sexual disgust and homonegativity. It could be argued that such an effect proves the flexible functionality of the BIS. When a given pathogen (e.g., COVID-19) is transmitted in a specific way (e.g., through respiratory droplets), the threat of becoming infected should motivate avoidance of people and situations that increase the risk of this particular contact (e.g., standing near coughing people). If gay persons are associated with sexually transmitted diseases (e.g., AIDS; Crandall et al., 1997; Pachankis et al., 2015), then there is no reason to expect that the threat of COVID-19 would motivate avoidance of gay men or lesbians. If we focused on the threat of AIDS, however, then we could expect that motivation.

To conclude, our short report provides some evidence confirming the predictions stemming from the behavioral immune system theory in predicting homonegative attitudes. It reaffirms the previous evidence indicating the pivotal role of disgust in disease-avoidance mechanisms, and specifying sexual disgust as the most important aspect when considering attitudes toward gay men and lesbians. It also emphasizes the functional flexibility of the BIS by demonstrating the moderating role of perceived vulnerability to disease. Finally, it shows for the first time that the threat of COVID-19 does not strengthen the relationship between disgust and homonegativity.

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: Open Science Framework: https://osf.io/976qp.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by The Ethical Review Board at SWPS University of

Social Sciences and Humanities, Faculty of Psychology in Sopot. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

AS and NF conceptualized and designed the research. NF conducted the research. AS analyzed and interpreted the data. AS, NF, and KG wrote the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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BRIEF RESEARCH REPORT
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Effects of Social Distancing During the COVID-19 Pandemic on Anxiety and Eating Behavior—A Longitudinal Study

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As social animals, humans need to live in groups. This contact with conspecifics is essential for their evolution and survival. Among the recommendations to reduce transmission of the new coronavirus (SARS-CoV-2) responsible for COVID-19 are social distancing and home confinement. These measures may negatively affect the social life and, consequently, the emotional state and eating behavior of individuals. We assessed the impact of the COVID-19 pandemic on the anxiety, premenstrual symptoms, and eating behavior of young women. Data collection was conducted in person (prepandemic—from March to December 2019) and online (during the pandemic—August 2020). A total of 71 participants, average age of 21.26 years (SD = 0.41), took part in the study. Trait anxiety during the pandemic was significantly lower than in the prepandemic period. Investigation of the "anxiety/stress" symptom of the Premenstrual Symptoms Screening Tool (PSST) revealed that this symptom was more severe before the pandemic. There was a decline in the desire for sweet and fatty foods during the pandemic. However, craving for traditional foods rose significantly in the same period. Uncontrolled and emotional eating were significantly lower during the pandemic. The results suggest that the pandemic may have had a positive impact on anxiety and eating behavior of the participants, which may be due to differences between urban and rural populations and the latter living with their families. These findings are important for raising a discussion regarding the effects of the current environment on the regulation of cognitive and dietary adaptations.

Keywords: COVID-19, social isolation, confinement, dietary behavior, mental health, human evolution

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INTRODUCTION

As social animals, human beings benefit from contact with co-specifics, since living in a group is an important strategy used by our ancestors to overcome daily challenges, which resulted in cognitive adaptations that support sociability (Dunbar, 2008, 2020; Lopes et al., 2018). Once basic needs are met, a more significant factor for the subjective and emotional well-being of most people seems to

be good relationships with friends and family. In addition, the size and quality of a person's social network also have a positive influence on mental health (Dunbar, 2017; Kenrick and Krems, 2018).

Similar to how our species evolved to live in groups, another clearly important psychological mechanism is activated in this context. The risk of dying from a contagious disease was a real and significant threat to our ancestors. However, a behavioral immune system, that is, a set of specific behaviors, may help us avoid diseases (Schaller and Park, 2011; Griskevicius and Kenrick, 2013; Ackerman et al., 2020). SARS-CoV-2 is a new coronavirus responsible for coronavirus disease 2019 (COVID-19) (Parlapani et al., 2020). In order to reduce virus transmission, social distancing and home confinement were recommended by health authorities and governments (Lakhan et al., 2020; Parlapani et al., 2020; Tang et al., 2020). However, distancing measures, even when added to activation of this behavioral immune system, may have a negative effect on the social life and emotional state of individuals (Ackerman et al., 2020; Akdeniz et al., 2020; Cornine, 2020; Di Renzo et al., 2020; Ingram et al., 2020; Shigemura et al., 2020; Volino-Souza et al., 2020; Wang et al., 2020; Zhou et al., 2020).

Thus, in addition to the protective recommendations against COVID-19, the fear of contracting the virus, and subsequently dying from it, uncertainty about disease control and vaccine availability, daily routine interruptions, economic loss, and constant exposure to negative news are factors considered highly responsible for the surge in mental health problems, such as anxiety (Akdeniz et al., 2020; Cornine, 2020; Di Renzo et al., 2020; Ingram et al., 2020; Kang et al., 2020; Ozamiz-Etxebarria et al., 2020; Shigemura et al., 2020; Volino-Souza et al., 2020; Wang et al., 2020; Zhou et al., 2020). In university students, anxiety symptoms have also been caused by concern about delays in academic activities and future job prospects (Akdeniz et al., 2020; Cornine, 2020; Zhou et al., 2020).

In principle, anxiety is a response that arises naturally as individuals are exposed to some everyday situations, serving as preparation for future events (Nesse, 2019a). However, when the response to these situations is no longer adequate (adaptive), anxiety can be pathological and present itself as a mental disorder, known as anxiety disorder. What differentiates adaptive anxiety from anxiety disorders are fear, emotional reaction, and excessive behavioral disturbances, which exist without adequate or proportional external stimulation to explain them and generally persist beyond the periods considered appropriate (Braga et al., 2010; American Psychiatric Association, 2014).

From an evolutionary point of view, it is necessary to consider that the demands of the current environment differ enormously from those in which the set of human development adaptations was selected. Thus, it is possible that an incompatibility between the evolved adaptation and the current environment favors the occurrence of these mental disorders, that is, the current environment does not drive the evolved mechanism in the way predicted (Kennair, 2003).

With respect to anxiety in women, in addition to the possible changes caused by the pandemic, the menstrual cycle also influences neurological and psychological functions. The hormonal variations that occur during the menstrual cycle, more specifically, the decline in estrogen and increase in progesterone that take place in the luteal phase or premenstrual period, may affect brain function, cognitive processes, emotional state, and appetite, among others. The symptoms associated with this phase can be variable or inconstant and generally include the following emotional signs: anger, irritability, anxiety, lack of concentration, and changes in mood and eating behavior (Johnson et al., 1995; Nissar et al., 2008).

Concerning the last point, stress and anxiety caused by social distancing, home confinement, the routine acquired during the pandemic, and partial or total loss of income (De Backer et al., 2021) may also influence eating behavior, having a negative effect on the amount and quality of the food consumed and access to it (Ammar et al., 2020; Cherikh et al., 2020; Górnicka et al., 2020; Naja and Hamadeh, 2020; Cummings et al., 2021). However, the psychological suffering caused by COVID-19 can also be related to positive eating behavior, as preparing food potentially works as an activity to relieve stress (Mosko and Delach, 2020; De Backer et al., 2021).

Many characteristics acquired by human beings through natural selection have reflected on dietary quality. Selective pressure has resulted in the foods obtained being composed of essential nutrients able to rapidly meet their nutritional needs. However, despite the maintenance of adaptive predispositions, over time, the reason for food intake was no longer exclusively to meet nutritional needs because current life conditions (such as the development of a series of diseases) have emerged (Zucoloto, 2011; Lopes et al., 2018; Nettersheim et al., 2018; Rantala et al., 2019).

Current life conditions that have a negative effect on mental health, causing stress and anxiety, can also be responsible for dietary changes (Ammar et al., 2020). In order to regulate and reduce negative emotions, these situations are generally associated with unhealthy foods, since due to the interaction between some foods and the central reward pathways, there is a propensity to desiring and consuming "tasty" foods with high levels of sugar, fat, and calories (Wardle et al., 2000; Sominsky and Spencer, 2014; Ingram et al., 2020). In line with this information, some research has observed an increase in total caloric intake (Ismail et al., 2020) and in candy intake (Deschasaux-Tanguy et al., 2020; Górnicka et al., 2020; Ismail et al., 2020; Cummings et al., 2021) during home confinement caused by COVID-19. However, Rodríguez-Pérez et al. (2020) described that home confinement promoted a low intake of sweets by the participants in their study.

In studies on eating behavior, the term food craving has been used to describe an "intense desire to eat a certain type of food" (Rogers and Smit, 2000) and is more associated with eating foods with high sugar content. The foundation for the strong preferences that many animals have for sweet foods results from their need to identify sources of metabolic fuel, especially glucose. In this respect, energy that is more readily available in food containing glucose would allow the brain to react to signals and symptoms caused by anxiety. However, the degree of sweetness does not provide quantitative information on glucose content, that is, energy (Beauchamp, 2016). Thus, the primary function

of preference for sweets may lie in the flavor of these foods, since the sensation of sweetness is generally associated with a pleasant experience or reward, not necessarily proportional to the glucose content present in the food (Beulens et al., 2004; Beauchamp, 2016).

It is noteworthy that in ancestral environments, sweet flavors were associated with fruits, yams, and honey. Thus, the preference and ingestion of foods considered sweet were not considered harmful to health. In this perspective, the sweet foods currently desired by humans can be considered evolutionarily incompatible, as they are produced with large amounts of processed sugars and lacking nutrients, and the physiological mechanisms that involve insulin and glucagon have not evolved to repeatedly metabolize abnormally large amounts of sugar (Li et al., 2018).

This trend to eat certain foods, excessively or not, which manifests itself as a response to some emotional states, is called emotional eating behavior or emotional eating (Ouwens et al., 2009; Serin and Koç, 2020). Considering anxiety during the premenstrual period and its relation with eating patterns, the preference/desire and increase in sweet food consumption that occur during this time (Gingnell et al., 2012) may be related to an attempt to modulate anxiety as a symptom attributed to the luteal phase of the menstrual cycle (Bernardi et al., 2005). In addition, from an evolutionary perspective, the desire and intake of caloric foods in the premenstrual period (reflecting proximal aspects, according to Tinbergen, 1963; Nesse, 2019b) may be due to the increased metabolic expense to prepare the body for reproduction (distal aspects— Tinbergen, 1963; Nesse, 2019b). The metabolic rate in the follicular phase is approximately 7% lower than in the luteal phase of the menstrual cycle (Strassmann, 1999).

In light of the above, the aim of the present study was to assess the impact of the pandemic caused by COVID-19 on anxiety, premenstrual symptoms, and eating behavior in young women. Our expectation was that the pandemic was related to an increase in the levels of anxiety and premenstrual symptoms and that it had an impact on eating behavior, intensifying emotional eating and the craving for certain foods, especially sweets.

MATERIALS AND METHODS

Participants and Procedures

The sample was composed of university students from rural Rio Grande do Norte state (RN), northeastern Brazil. The study occurred in two stages, one in person and one online. During the first stage, volunteers were recruited through personal contact and advertising the study on posters, in classrooms, and other common areas of the university. The second stage was conducted on the internet using the Google Forms platform and the link was shared through WhatsApp and by email (according to information reported by the participants in the first stage). The study is in accordance with Brazilian National Health Council and the Declaration of Helsinki and was approved by the Research Ethics Committee for the Faculty of Health Sciences of Trairi of the Federal University of Rio Grande do Norte (Protocol number CASE: 91161718.0.0000.5568; Research authorization: 2.830.540).

Included were volunteers aged 18 years and older who gave written informed consent to participate. Students using anxiolytics or antidepressants (including natural) were excluded from the study. The in-person stage, which occurred from March to December 2019 (prepandemic period), included 136 participants, who responded to five questionnaires: sociodemographic, Brazilian Food Craving Inventory (FCI-Br), the Brazilian version of the Three Factor Eating Questionnaire—R21 (TFEQ-R21), State Trait Anxiety Inventory (STAI), and the Brazilian version of the Premenstrual Symptoms Screening Tool (PSST). In the online stage, conducted in August 2020 (during the pandemic), 5 months after the implementation of confinement measures in Rio Grande do Norte state (RN), 71 students responded online to the same questionnaires applied in the first stage, adding whether they had been diagnosed with COVID-19 and answering a question related to home confinement (**Figure 1**).

Measures and Instruments

Nutritional Status Assessment

Prepandemic nutritional status was assessed using body mass index (BMI), which was calculated from the weight and height self-reported by the participants in the sociodemographic questionnaire [validation of BMI from self-reported measures, in this population, was performed in the study of Lima et al. (2018)].

Assessment of Eating Behavior

The FCI-Br and the Brazilian version of the TFEQ-R21 were used to assess eating behavior. The FCI-Br was validated by Medeiros et al. (2017) and was created based on the Food Craving Inventory (White et al., 2002), which categorizes and identifies foods that are most related to craving, investigating the frequency of these episodes in the previous month. The FCI-Br consists of 23 foods commonly related to craving, divided into three categories: high fat content (pizza, fried pastry, bacon, salty packaged snacks, lasagna, sandwich/hamburger, *coxinha*, and French fries), sweets (cookies; dulce de leche; chocolate; condensed milk pudding; candy such as hard candy, lollipop, and jelly beans; ice cream; *brigadeiro*; sweet pie; and cake), and traditional foods (bread, barbecue/grilled meat, *farofa*, cheese, beans/*feijoada*, and steak) (Medeiros et al., 2016a; Meule, 2020).

The TFEQ was developed by Stunkard and Messick (1985) to determine cognitive restraint (CR), disinhibition, and susceptibility to hunger in adults. The first version of the TFEQ consisted of 51 items, but later studies developed shorter and psychometrically improved versions of this questionnaire, such as the TFEQ-R21. The shorter TFEQ-R21 version, adapted and translated to Brazilian Portuguese by Medeiros et al. (2016b), was created based on the TFEQ-51, containing 21 items and assessing three eating behavior dimensions: emotional eating (EA), uncontrolled eating (UE), and CR. The EA scale measures the susceptibility of consuming foods as a response to emotional stress and negative mood states. UE behavior is the tendency to lose control overeating when feeling hungry or exposed to external stimuli (for example very tasty food), even in the absence

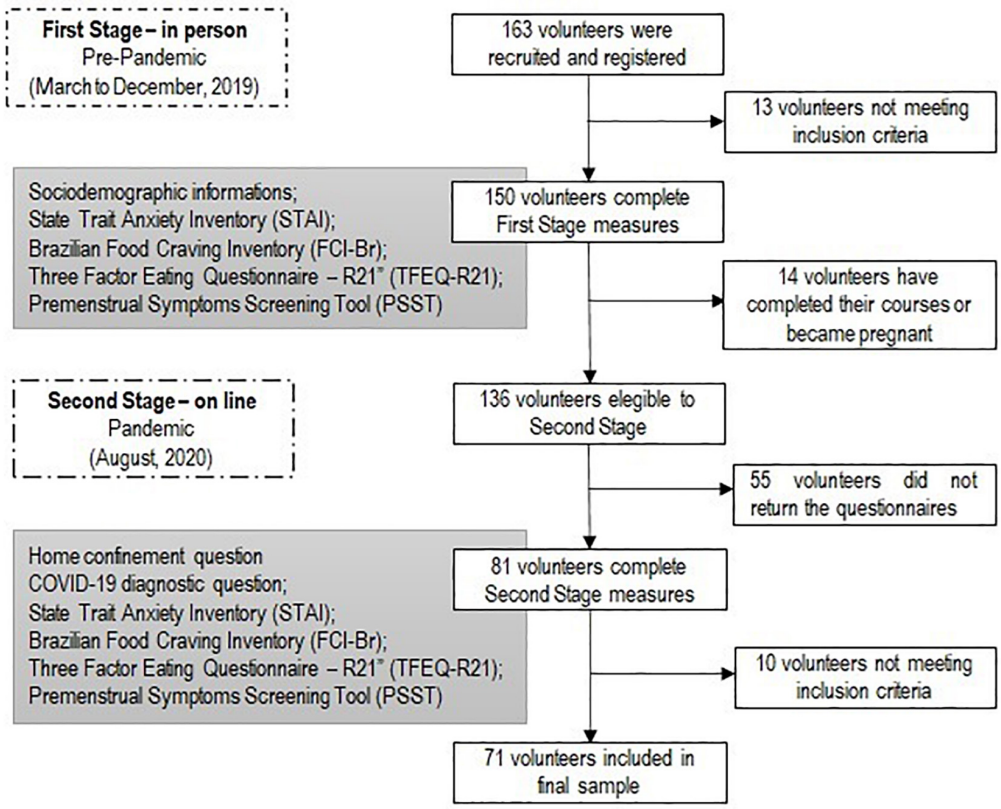

FIGURE 1 | Diagram for the participants' recruitment and inclusion in the study.

of hunger. Finally, CR is characterized as the limitation (cognitive and self-imposed) of food ingestion in order to control body weight (Medeiros et al., 2016b, 2019).

Assessment of Anxiety

The State-Trait Anxiety Inventory (STAI) was used to assess anxiety. The STAI was developed by Spielberger et al. (1970) and translated and adapted for Brazil by Biaggio and Natalício (1979). The tool is used to assess relatively stable anxiety. It consists of 20 statements concerning personal feelings, where the subjects report on the frequency at which these feelings generally occur. Each statement is answered on a scale varying from 1 (almost never) to 4 points (almost always), and each volunteer obtained scores between 20 and 80 (Spielberger et al., 1970; Vigneau and Cormier, 2008; Leal et al., 2017).

Assessment of Premenstrual Symptoms

Premenstrual symptoms were assessed using the Brazilian version of the PSST. The PSST was developed and validated for Brazil by Câmara et al. (2016). This instrument identifies the presence of premenstrual symptoms (PMS) and premenstrual dysphoric disorder (PMDD) and is composed of 19 items subdivided into two domains. Domain I consists of 14 physical and psychological manifestations of PMDD described in the diagnostic and statistical manual of mental disorders (DSM-IV). Among the symptoms assessed in this domain is "anxiety/stress." Domain II is composed of five items that assess the functional impact of PMS. Each item is answered according to a four-point Likert scale (0 = absent; 1 = mild; 2 = moderate; 3 = severe) (Steiner et al., 2003; Henz et al., 2018).

Assessment of Home Confinement

The participants answered a question about how much people were leaving home (for any purpose) during confinement, using a five-point Likert scale (0 = much less than usual; 1 = less than usual; 2 = the same, no change; 3 = more than usual; 4 = much more than usual).

Data Analysis

Data normality and homogeneity were verified by the Kolmogorov–Smirnov and Shapiro–Wilk tests, respectively. Normally distributed variables were compared using the paired Student's *t*-test, and for the others, the Wilcoxon signed rank test was used. The relation between variables was determined by the chi-squared test. The results were considered significant at a 95% significance level ($p < 0.05$).

RESULTS

A total of 71 subjects, with an average age of 21.26 years (SD = 0.41) and mean prepandemic BMI of 22.93 kg/m^2

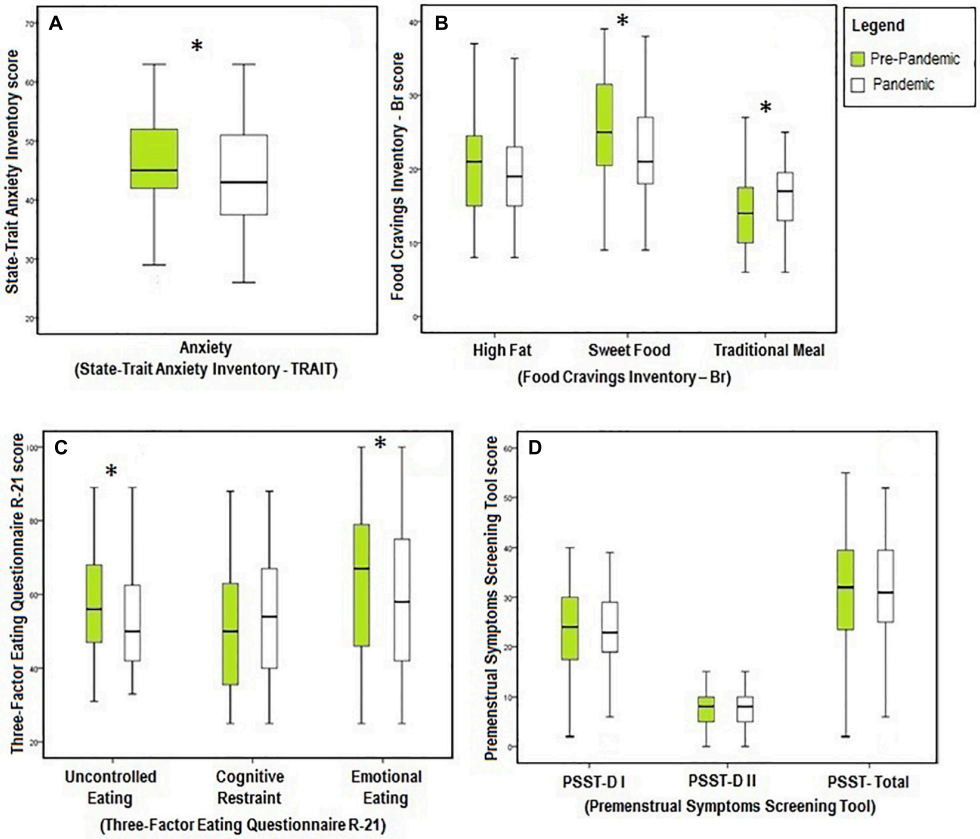

FIGURE 2 | Result of the main measures observed in the study. **(A)** Trait anxiety before and during the pandemic. **(B)** Food craving before and during the pandemic. **(C)** Dimensions of eating behavior before and during the pandemic. **(D)** Premenstrual symptoms by domain and total before and during the pandemic. PSST, Premenstrual Symptoms Screening Tool; DI, domain I from PSST; DII, domain II from PSST; $*p < 0.05$.

(SD = 0.44), indicating a predominance of eutrophic nutritional status in the evaluated group (88.7% of participants), took part in the study. Three of the students (4.3%) had been infected by COVID-19.

Anxiety

With respect to anxiety, the STAI revealed that trait anxiety during the pandemic (44.4 ± 8.4 points) was significantly lower [$t(70) = 2.023$, $p = 0.047$, $r = 0.23$, $n = 71$] than in the prepandemic period (46.4 ± 8.7 points) (**Figure 2A**). It is important to underscore, reinforcing the stability of the measure, that the score remained classified as moderate anxiety despite the significant difference.

The total PSST score showed no change in the presence and severity of premenstrual symptoms between the two periods analyzed [$t(70) = -0.013$, $p = 0.990$, $n = 71$] (**Figure 2D**). However, the "anxiety/stress" symptoms of this tool revealed that it was more severe in the students before the pandemic [$\chi^2(2) = 8.884$, $p = 0.012$, **Table 1**].

Eating Behavior

Considering food craving, there was a significant decline in the desire for sweet foods during the pandemic [25.0 (20.5–31.5) versus 21.0 (18.0–27.0), $z = -3.776$, $p < 0.001$, $r = 0.45$, $n = 71$]. The craving for traditional foods rose significantly in the same period [14.0 (10.0–17.5) versus 17.0 (13.0–19.5), $z = -3.203$, $p = 0.001$, $r = 0.38$, $n = 71$] (**Figure 2B**).

In relation to the three dimensions of eating behavior assessed by TFEQ-R21, uncontrolled [56.0 (47.0–68.0) versus 50.0 (42.0–62.5), $z = -2.771$, $p = 0.006$, $r = 0.33$, $n = 71$] and emotional eating [67.0 (46.0–79.0) versus 58.0 (42.0–75.0), $z = -2.229$, $p = 0.026$, $r = 0.26$, $n = 71$] were significantly lower during the pandemic. Cognitive restraint increased during this time, but the difference was not significant (**Figure 2C**).

Actions During the Pandemic

In relation to "outings during social distancing," 49 (69.0%) of the participants left their home "much less than usual," 21 (29.6%) "less than usual," and 1 (1.4%) "more than usual."

As shown in **Figure 3**, when analyzed separately, differences were identified between the prepandemic and pandemic period only in the group that left their home "much less than usual," which demonstrated a decline in craving for sweet foods [26.0 (22.0–33.0) versus 21.0 (19.0–29.0), $z = -3.616$, $p < 0.001$, $r = 0.52$, $n = 49$] and uncontrolled [58.0 (50.0–69.0) versus 50.0 (44.0–61.0), $z = -2763$, $p = 0.006$, $r = 0.39$, $n = 49$] and emotional

eating [67.0 (50.0–79.0) versus 58.0 (46.0–75.0), $z = -1.982$, $p = 0.047$, $r = 0.28$, $n = 49$], as well as an increase in craving for traditional foods [26.0 (22.0–33.0) versus 21.0 (19.0–29.0), $t(48) = -2.733$, $p = 0.009$, $r = 0.37$, $n = 49$].

When the prepandemic and pandemic periods were compared, no significant differences were found in terms of trait anxiety (**Figure 3A**), presence and severity of premenstrual symptoms (**Figure 3B**), "anxiety/stress" symptom, craving for fatty foods, and food restraint.

DISCUSSION

Stressful situations observed in contemporary environment may be associated with the desire to eat foods with high sugar or fat contents, since there is an attempt to attenuate psychological stress by consuming these foods (Rantala et al., 2019). In this respect, the spread of the pandemic and the protective measures adopted, such as social isolation and distancing, would compromise mental health and lead to the intake of unhealthy foods (Wardle et al., 2000; Sominsky and Spencer, 2014; Ammar et al., 2020; Ingram et al., 2020).

Unlike the above-described expectation, the present study found that the anxiety trait remained moderate before and during the pandemic and that the "anxiety/stress" symptom was milder during the pandemic. It also revealed a decrease in craving for sweet foods and an increase for traditional foods during the same period, in addition to a decline in uncontrolled and emotional eating.

Pandemics cause concern and anxiety is a commonly observed psychological problem in these situations. Reinforcing this fact, it was reported that in China (Wang et al., 2020), Spain (Ozamiz-Etxebarria et al., 2020), Japan (Shigemura et al., 2020), Wuhan, and Scotland, COVID-19 caused mental problems in the population (Ingram et al., 2020).

However, although the fear of contracting the virus is a continuous stressor that stimulates the appetite and emotional eating mediated by glucocorticoids (Sominsky and Spencer, 2014), biological (Rantala et al., 2018), sociocultural, economic, and environmental factors may affect the mental health of individuals differently in stressful situations (Liu et al., 2020). For example, confinement can produce healthier eating habits, due to the greater time available for cooking and fewer temptations to eat harmful foods (Ingram et al., 2020; López-Bueno et al., 2020; Rodríguez-Pérez et al., 2020).

With respect to home confinement, our results corroborate these explanations in that the participants who leave home "much less than usual" during the pandemic reported a decline in craving for sweet foods, while craving for traditional foods increased, likely due to the greater exposure to this type of food.

In this respect, an electronic survey conducted in Poland (PLifeCOVID-19) revealed that 48% of those interviewed reported an increase in the consumption of home-cooked meals, attributed to the increased possibility of preparing a meal at home or more free time to take care of health during home confinement (Górnicka et al., 2020). Similarly, the COVIDiet study (Rodríguez-Pérez et al., 2020) carried out with 7,514 Spanish adults showed that during COVID-19 confinement, there was significant adherence to the Mediterranean diet (characterized by the consumption of extra virgin olive oil, whole grains, and vegetables, with low intake of sweets, red meat, and processed foods; Bach-Faig et al., 2011).

Another cross-sectional online survey carried out in 38 countries, which investigated three domains of food literacy behavior (food planning, selection, and preparation), observed that during the COVID-19 pandemic, the perception of having more time was associated with increases in planning, selecting, and preparing healthier foods for women and men and that policies for staying at home or working at home were positively related to planning and preparing healthier foods for both sexes (De Backer et al., 2021).

On the other hand, an online survey on mental health and lifestyle during home confinement (ECLB-COVID19), involving 35 research organizations from Europe, North Africa, Western Asia, and the Americas, found an unhealthy dietary pattern (type of food, uncontrolled eating, between-meal snacks, and number of main meals) during home confinement (Ammar et al., 2020). Another study with 1,012 participants from the United Arab Emirates showed a significant increase in the percentage of subjects that consumed primarily home-cooked meals, and that the foods selected were not nutritious, with the daily presence of sweets and savory snacks, which was also attributed to restricted food access (Ismail et al., 2020).

De Backer et al. (2021) also observed that staying at home was negatively associated with the selection of healthier foods for women and men. In addition, another relevant finding was a greater psychological distress observed in women during the COVID-19 pandemic and that this psychological distress was related to decreased planning, selection, and preparation of healthier foods. Among men, there was an increase in the preparation of healthier meals when psychological suffering increased. This result can be explained by the possibility that, during the pandemic, psychological suffering became a barrier to the daily cooking of women, but for men, it was an alternative to relieve stress.

It is important to underscore a significant aspect of the present study, namely that food intake was not measured, but rather eating behavior. Particularly with respect to craving, the

TABLE 1 | Evaluation of anxiety/stress from the Premenstrual Symptoms Screening Tool (PSST).

	Prepandemic	During the pandemic
	n = 71	*n* = 71
Anxiety/stress[a]*		
Absent and mild	18 (25.4%)	24 (33.8%)
Moderate	29 (40.8%)	38 (53.5%)
Severe	24 (33.8%)	9 (12.7%)

*The results are expressed as n (%). [a]Extracted from domain I from the Premenstrual Symptoms Screening Tool. *p < 0.05 in Pearson's chi-squared test.*

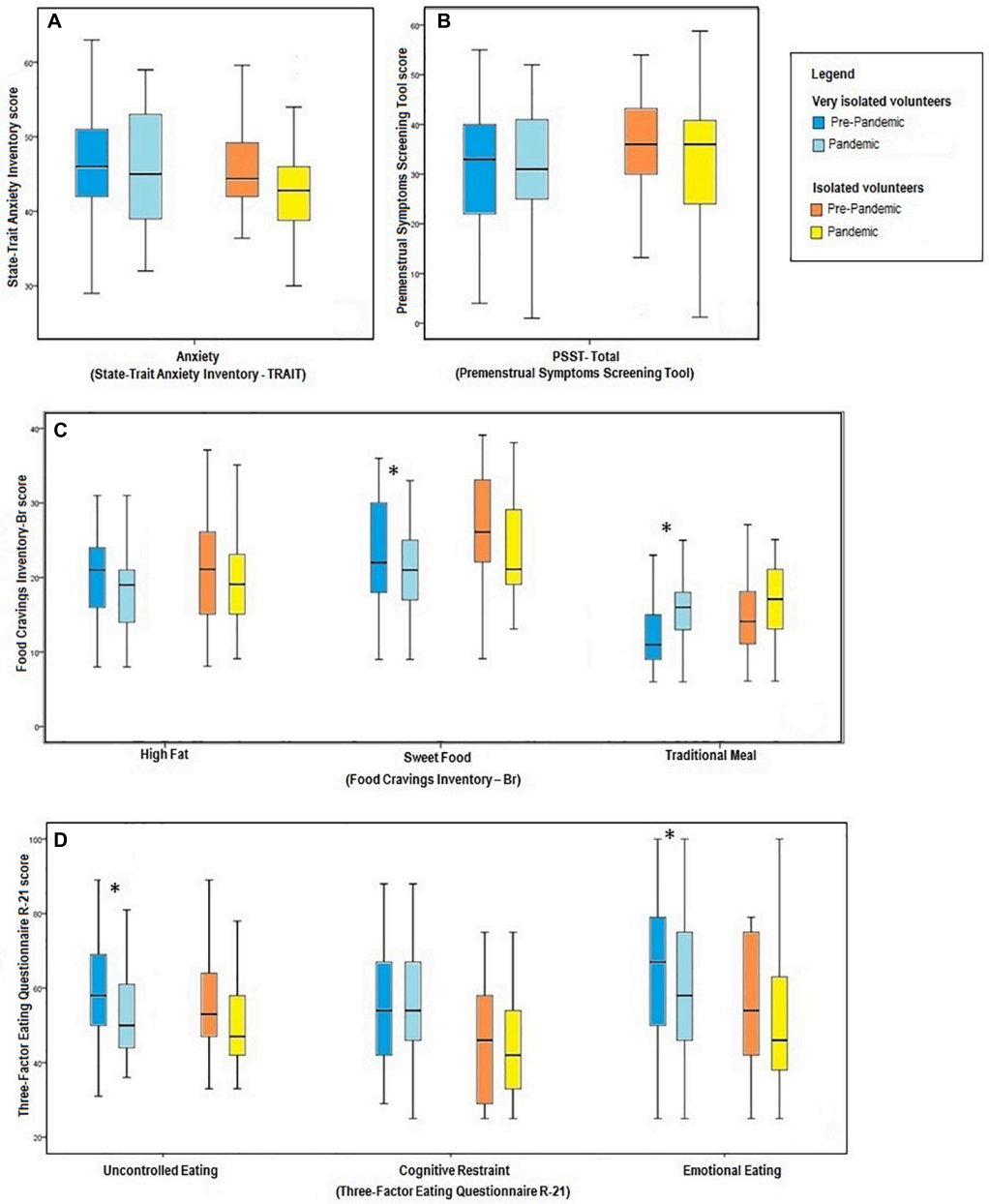

FIGURE 3 | Comparison between the different measures obtained in the study, considering the confinement at home of participants during the pandemic. **(A)** Trait anxiety according to confinement at home. **(B)** Premenstrual symptoms according to confinement at home. **(C)** Food craving according to confinement at home. **(D)** Dimensions of eating behavior according to confinement at home. PSST, Premenstrual Symptoms Screening Tool; *$p < 0.05$.

decrease and increase in craving for sweets and traditional foods, respectively, indicate a change in the desire to eat a certain type of food, suggesting an intriguing perspective for the future eating habits of these women.

In relation to the impact of the pandemic on dietary behavior, 638 undergraduate and former undergraduate female students from King Saud University in Saudi Arabia were studied. In this survey, approximately half the women in the sample reported emotional eating (EE) during the COVID-19 pandemic. A total of 335 women (52.5%) reported low EE, while 202 (31.7%) were in the moderate and 101 (15.8%) in the high EE group. The study also demonstrated that eaters with the highest EE score had a trend to report anxiety. However, no significant association was observed between anxiety and EE. One possible explanation is that anxiety provoked by COVID-19 was an acute stressor, thereby reducing appetite and emotional eating (Al-Musharaf, 2020). It is important to emphasize that these reports were compiled over a short period of time after the onset of the pandemic.

In the United States, the study by Cummings et al. (2021) demonstrated that during the COVID-19 pandemic, American adults increased the addition of sugars to foods by 14%, but despite this increase in sugar intake, there was no increase in total food consumption in response to the stress caused by the pandemic. So, the reason for this sharp change in eating behavior may be due to the purchase of more nonperishable processed foods during this period.

Given these different results, a key factor to consider is that the participants of the present study are university students from a rural area of the state, but most come from small towns in the region and are only living in the city where the university is located for study purposes. Living outside the family home has been a factor related to poor quality of diet and emotional and anxiety disorders in undergraduate students (Papadaki et al., 2007; Zurita-Ortega et al., 2018; Cao et al., 2020). Thus, despite the protective measures and the concern about the new coronavirus, returning to their hometowns to be with their families may explain the lower anxiety and eating behaviors observed.

As humans are highly social animals, the response to the threat of infection by COVID-19 causes the desire for contact and social support, especially in relation to loved or vulnerable people, such as family members (Dezecache et al., 2020). The loss of this type of social contact can have an impact on subjective well-being (Paredes et al., 2021), with a negative response from the nervous system, since the activation of some psychological mechanisms in contexts of food sharing and other forms of cooperation so important in the evolutionary history of our species is limited (Ringer et al., 2019).

This influence seems to be supported by evidence from the Spanish study COVIDiet, which found that living at home with one's family may be associated with a healthier diet (Rodríguez-Pérez et al., 2020). A study with 7,143 Chinese university students reported that living with families/parents during the pandemic may be a protective factor against anxiety (Cao et al., 2020). In addition, it is believed that people who frequently eat with others are happier and more satisfied with their lives, since eating socially releases endorphins, which may promote the same positive effect as that caused by physical exercise (Cohen et al., 2010; Dunbar, 2017).

One aspect that deserves attention is the opportunity we had to observe the behavior of a group outside of large urban centers. A number of factors indicate that living in small cities may also protect individuals against stress and anxiety. Most cases of COVID-19 occurred in the state capitals, resulting in greater sensitivity and vulnerability to psychosocial impacts of the pandemic on the residents of these communities. The high population densities of the capitals facilitate the transmission of the virus, producing stress due to the increased perceived risk of infection. Moreover, living in large cities may also raise the likelihood of access to communication and information. A study performed with 3,068 subjects in China, consisting of 1,928 urban dwellers and 1,140 rural residents, reported a significantly higher prevalence of mental health problems associated with the COVID-19 pandemic in urban individuals compared with those who live in rural environments (Liu et al., 2020).

In addition to the reasons explained above, the higher incidence of mental health problems in individuals living in urban environments may be due to an evolutionary incompatibility, as different from the ancestral world and small cities, urban centers are marked by a greater dispersion of families, less exposure to nature, sleep disturbances, greater sedentary lifestyle, and greater intake of processed foods (Rantala et al., 2021). As societies globalize and human-induced environmental changes increase rapidly, evolutionary mismatches are becoming increasingly prevalent (Li et al., 2018).

The protective measures implemented due to the COVID-19 pandemic may have aggravated the practice of unhealthy lifestyles, such as physical inactivity and the consumption of processed foods. In this sense, in addition to the stress and anxious symptoms caused by the incompatibility of biological and cognitive expectations between the ancestral and the contemporary environment of urban centers (Kavanagh and Kahl, 2018), the negative changes in mood can also be related to neuroinflammation caused by current and evolutionarily new lifestyles, as factors such as unhealthy eating and low or no physical activity favor the increase in the serum amount of proinflammatory cytokines (Rantala et al., 2018, 2021).

The influence of returning to their families and the fact that the study population live in small cities seem to be essential to understanding the results of the present study, since they contradict other research, which found an increase in anxiety levels among university students in several countries (Akdeniz et al., 2020; Cornine, 2020; Wang et al., 2020; Zhou et al., 2020). In our study, we recorded a reduction in anxiety trait expression. Although we are referring to a trait, and therefore, with less expectation of change, Cohen et al. (2014) argue that it is possible that there are changes in the expression of a trait, especially when we consider the nature of the situations in which the trait is expressed. Dealing with the pandemic situation has been one of the greatest experiments that humanity has been facing. We still have no way of accurately measuring the psychological effects that such a situation can have in the short, medium, and long term.

This study has several limitations due to the following factors: not investigating the economic situation and exposure to pandemic-related information of the participants; the data being self-reported, which may have introduced memory bias; and the online stage having occurred at a time when some of the social distancing measures had been relaxed (beginning of the reopening of commercial stores and nonessential services). Nevertheless, the study exhibits strong points that produced robust results. We compared data collected in the prepandemic and pandemic periods, and the sample was non-urban (less studied in other research) and composed of young women, who are more predisposed to developing mental disorders. Also, as a positive aspect, the study was carried out in a sample of the Latin American population that was little studied. Most research are conducted in North America or Western Europe (Henrich et al., 2010). Thus, in order to obtain representativeness regarding

human species diversity, science needs to include more cultures (Barrett, 2020), focusing particularly on less studied populations. Still, at a time when public policies for coping with COVID-19 have been formulated and implemented quite quickly, the present study warns about the importance of studying differences between urban and rural environments. Different contexts can generate different responses to the current state of the world pandemic, reflecting the need for differentiated strategies in health care for the population.

In conclusion, our findings suggest that the pandemic may have had a positive impact on the anxiety and eating behavior of the participants, which may be due to the differences between urban and city dwellers and living with families. These findings demonstrate the importance of discussing the effects of the current environment on the regulation of cognitive and dietary adaptations, as well as emphasizing the importance of diversifying participants, since contexts in which we live are essential to understanding possible variations in the behavioral expression of our species.

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 Research Ethics Committee for the Faculty of Health Sciences of Trairi of the Federal University of Rio Grande do Norte under protocol number 2.830.540. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

FF, AM, and FL conceived and designed the study, conducted the statistical analysis, and wrote and revised the manuscript. FF organized the database. All the authors contributed to the article and approved the version submitted.

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Unrealistic Optimism and Risk for COVID-19 Disease

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Risk perception and consequently engagement in behaviors to avoid illness often do not match actual risk of infection, morbidity, and mortality. Unrealistic optimism occurs when individuals falsely believe that their personal outcomes will be more favorable than others' in the same risk category. Natural selection could favor overconfidence if its benefits, such as psychological resilience, outweigh its costs. However, just because optimism biases may have offered fitness advantages in our evolutionary past does not mean that they are always optimal. The current project examined relationships among personal risk for severe COVID-19, risk perceptions, and preventative behaviors. We predicted that those with higher risk of severe COVID-19 would exhibit unrealistic optimism and behave in ways inconsistent with their elevated risk of morbidity and mortality. Clinical risk scores for severe COVID-19 were calculated and compared with COVID-19 threat appraisal, compliance with shelter-in-place orders (March 13–May 22, 2020) and travel restrictions, compliance with public health recommendations, and potential covariates like self-rated knowledge about COVID-19 in a robust dataset including 492 participants from McLennan County, TX, USA. While those with high clinical risk acknowledged their greater likelihood of experiencing severe illness if infected, they actually reported lower perceived likelihood of becoming infected in the first place. While it is possible that those with higher clinical risk scores truly are less likely to become infected, the pattern and significance of these results held after controlling for possible occupational exposure, household size, and other factors related to infection probability. Higher clinical risk also predicted more recent travel within Texas and lower distress during the pandemic (i.e., feeling less stressed, depressed, and helpless). Additional behavioral data suggested that those with higher clinical risk scores did not generally behave differently than those with lower scores during the shelter-in-place order. While unrealistic optimism may provide some short-term psychological benefits, it could be dangerous due to improper assessment of hazardous situations; inferring that optimism bias has evolutionary origins does not mean that unrealistic optimism is "optimal" in every situation. This may be especially true when individuals face novel sources (or scales) of risk, such as a global pandemic.

Keywords: unrealistic optimism, risk perception, COVID-19, SARS–CoV–2, optimism bias, pre-existing condition

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INTRODUCTION

The spread of the SARS CoV-2 virus since late 2019 has generated a public health crisis, creating economic uncertainties (Pak et al., 2020), interrupting well-established food supply chains (Rizou et al., 2020), and ultimately resulting in large scale hospitalizations and deaths (Meyerowitz-Katz and Merone, 2020; Reese et al., 2020; Weinberger et al., 2020). The SARS-CoV-2 virus transmitted rapidly around the globe, resulting in millions of cases of COVID-19 disease. Although this serious and persistent threat remains, individuals' perceptions of risk and, consequently, their engagements in behaviors to avoid illness (e.g., wearing face coverings, social distancing, hygiene) have often not matched their own actual degree of risk of infection, morbidity, and mortality. For example, many people refuse to wear face coverings, even within healthcare facilities (Lehmann and Lehmann, 2020). Others continue to attend large gatherings, despite findings that these events confer considerable risk of SARS-CoV-2 virus exposure (Ebrahim and Memish, 2020; Majra et al., 2020; Sassano et al., 2020).

In the present project, we sought to build on these findings by examining relationships among individuals' personal risk for severe COVID-19 disease, risk perceptions, and preventative behaviors in a large community cohort. Specifically, we calculated clinical risk scores for severe COVID-19 disease and compared them to individuals' own perceptions of their risk. Further, we examined whether clinical risk scores were related to compliance with shelter-in-place orders, travel restrictions, and public health recommendations, as well as reported distress during the pandemic. Combining insights from the evolutionary and cognitive sciences, we predicted that those with a high clinical risk for severe COVID-19 disease would exhibit unrealistic optimism, characterized by an underestimation of their personal vulnerability and behaving in a manner inconsistent with their elevated risk of morbidity and mortality.

Unrealistic Optimism

Personal risk reduction relies on factors such as belief about the likelihood of an adverse event taking place and belief about the severity of that event (Rippetoe and Rogers, 1987; Floyd et al., 2000; Milne et al., 2000). Estimation of the probability and severity of a noxious event is important for assessing the relative costs and benefits of taking steps to decrease the event's likelihood. For example, underestimating one's risk may result in failure to prevent an avoidable negative outcome. On the other hand, overestimating one's risk may yield opportunity costs, that is, probable gains lost in the process of risk mitigation.

Despite these potential costs associated with inaccurate risk assessment, many people experience positive illusions regarding their individual risk in which they underestimate their own likelihood of experiencing negative outcomes (McKay, 2009). This tendency for individuals to falsely believe that their personal outcomes will likely be more favorable than others' in the same risk category is called "optimism bias" or "unrealistic optimism" (Sharot, 2011; Shepperd et al., 2015; Jefferson et al., 2017). Given that these terms are often used interchangeably in the literature, we henceforth refer to this bias as unrealistic optimism (Jefferson et al., 2017). Research has found that unrealistically optimistic beliefs are defined by their stability, persisting through selective attention for new information that confirms positive beliefs while disregarding information that contradicts the beliefs (Sharot et al., 2011). Moreover, these beliefs are genuinely accepted as truth by the individual (Jefferson et al., 2017).

The phenomenon of unrealistic optimism is widespread, applying to a variety of situations from health to stock market trading (Makridakis and Moleskis, 2015; Reyes-Velázquez and Sealey-Potts, 2015). Examples include an individual's beliefs that they are more likely than other players to win when rolling dice at a casino, or a married couple's tendency to underestimate the probability that their marriage will end in divorce relative to other couples (Jefferson et al., 2017). Even non-human animals, such as European starlings and mice, exhibit unrealistic optimism in certain choice tasks (Harding et al., 2004; Matheson et al., 2008).

Evolution and Unrealistic Optimism

Why is unrealistic optimism so common? It is difficult to imagine that underestimating risk, a potential opponent, or the difficulty of a task would be beneficial or evolutionarily adaptive. However, unrealistic optimism remains entrenched across human populations. A wide body of research has found that optimism, more generally, is linked to many positive health outcomes. For example, optimism is associated with a lower prevalence of high blood pressure across multiple populations (Räikkönen et al., 1999; Räikkönen and Matthews, 2008). Further, a recent meta-analysis identified a connection between optimism and both lower risk of cardiovascular events and all-cause mortality (Rozanski et al., 2019).

Regarding unrealistic optimism more specifically, insights from the evolutionary sciences indicate that selection could favor overconfidence as long as the benefits of unrealistic optimism outweigh its costs. Specifically, game theory models reveal that overconfidence can emerge as an evolutionarily stable strategy across a wide range of environments, and should be strongest under increasingly uncertain conditions (Johnson and Fowler, 2011). Unbiased risk estimation, on the other hand, is predicted by this model to be stable only under a limited set of specific conditions (Johnson and Fowler, 2011). These findings suggest that unrealistic optimism confers tangible benefits that favor its selection, particularly in environments characterized by risk and uncertainty.

Error Management Theory (EMT), an evolutionary framework for understanding cognitive biases (Nettle, 2004; Haselton and Nettle, 2006; McKay, 2009; Johnson and Fowler, 2011), provides key insights into the benefits of unrealistic optimism under uncertainty. Due to volatility in the environment and constraints on perception, totally accurate assessment of threat, and prediction of outcomes related to that threat, are often difficult or impossible. Under uncertainty, errors in judgment usually fall into one of two categories: false positives (i.e., assuming a threat exists when it does not) or false negatives (i.e., assuming a threat does not exist when it does). EMT posits that selection will favor bias toward the less costly type of error (Haselton and Buss, 2000; Haselton and Nettle, 2006). An analogy often used to describe such patterns of

error management is the smoke detector (Nesse, 2001; Haselton and Nettle, 2006). Of course, it would be best to have a very accurate smoke detector that can perfectly distinguish between burned toast and actual fire in an apartment. However, errors are unavoidable, and it is imperative that the smoke detector always senses a real fire. Accordingly, the smoke detector alarm, from time to time, will go off when we burn toast (false positive), but it rarely fails to go off in the event of an actual fire (false negative).

This framework may also help explain unrealistic optimism. Selection could favor biases toward "optimistic error" if true probabilities of success are incompletely known, and erring on the side of optimism provides greater benefits and/or bears fewer costs than erring on the side of pessimism (Haselton and Nettle, 2006; Jefferson, 2017; Jefferson et al., 2017). For example, due to males' higher reproductive variance relative to females' (i.e., in sexually-reproducing species with greater obligate female investment in offspring), the costs associated with missing out on mating opportunities are especially high for males, exceeding the costs of wasting energy on unsuccessful mating pursuits (Trivers, 1972; Alcock, 1993). EMT then proposes that males should be more prone to false positive, rather than false negative, errors when searching for mating opportunities. In other words, men should be unrealistically optimistic about women's interest in them. Consistent with this prediction, research has found that men, but not women, tend to overperceive cues of interest from the opposite sex (Haselton, 2003).

More generally, studies have found that positive illusions—such as unrealistic optimism—also yield psychological benefits in the face of risky or uncertain situations (Taylor and Brown, 1994; McKay, 2009; Makridakis and Moleskis, 2015), increasing motivation and promoting resilience in response to adversity (Bénabou and Tirole, 2002; Johnson and Fowler, 2011; Kleiman et al., 2017). For example, research has found that individuals who are unrealistically optimistic about how positively they will feel in the future are better able to handle stress (Colombo et al., 2020). Others have shown that college students with more optimistic expectations for their academic performance invest more quality effort into studying and are more satisfied with their decision-making (Lench et al., 2021). In sum, amid uncertainty, unrealistic optimism may yield benefits in the form of promoting resilience and motivating adaptive behaviors (McKay, 2009).

Maladaptive Optimism

While EMT provides a useful framework for understanding optimistic errors, there are arguments against evolutionary accounts of unrealistic optimism. Jefferson (2017) presents three potential problems with reducing unrealistic optimism to the outcome of an evolutionary cost-benefit analysis as is done in EMT. First, unrealistic optimism about health risks may lead to behaviors that contribute to morbidity and mortality. It is difficult to imagine that such costs are outweighed by the costs of assuming the worst in such scenarios. For example, one study found that in individuals with type II diabetes, greater optimism regarding future heart attack risk was actually associated with a higher incidence of lifestyle factors (e.g., smoking) that increase the likelihood of cardiovascular disease (Karl et al., 2020). A separate study found that smokers who were unrealistically optimistic about their lung cancer risk were less likely to have a smoking cessation plan than those who were less optimistic (Dillard et al., 2006).

Second, unrealistic optimism may lead individuals to believe that a positive result will occur even if they do not take action. In other words, unrealistic optimism might lead to complacency (Jefferson, 2017). Consistent with this possibility, a survey of 100 college students found that of 45 different health- and life-threatening events, participants showed an optimism bias for 34 of them. Further, unrealistically optimistic evaluations of risk from these hazards were associated with reduced worry about the occurring events (Weinstein, 1982), suggesting that overconfidence about one's likelihood of experiencing health problems may reduce motivation to take the steps necessary to mitigate risk. Many have even blamed unrealistic optimism for inadequate preparation for natural disasters or financial bubbles (Johnson and Levin, 2009; Johnson and Fowler, 2011; Shepperd et al., 2015; Glöckner, 2016; Michailova and Schmidt, 2016).

Lastly, Jefferson (2017) suggests that there exist many proximate moderators of unrealistically optimistic tendencies that are not accounted for by EMT. While the existence of these moderators does not necessarily contradict EMT, it suggests that factors other than the cost-benefit ratio of false positives and false negatives also influence optimism. Namely, better access to information, concerns about accountability, and mood states each affect optimistic beliefs (Sweeny et al., 2006). Perhaps an even more troubling moderating factor is that it is often those at the highest risk for adverse outcomes who are most unrealistic about their circumstances (Ferrer et al., 2012; Morgan et al., 2019; Dolinski et al., 2020). For instance, one study found that individuals who were more optimistic about their future risk for heart disease actually had greater intima-media thickness, an early marker of atherosclerosis (Ferrer et al., 2012). Others found that young people tend to underestimate their risk of household accidents relative to their older counterparts, despite being much more likely to experience these accidents (Morgan et al., 2019).

A similar pattern has been observed in the context of the current pandemic. For example, one study found that men, in particular, were unrealistically optimistic about their likelihood of SARS-CoV-2 infection (Dolinski et al., 2020), despite having a higher risk of infection and mortality from COVID-19 than women (Chakravarty et al., 2020). This is of grave concern because unrealistic optimism about one's likelihood of infection from the SARS-CoV-2 virus or severe illness from COVID-19 disease, may translate into dire consequences for those with high risk of infection, morbidity, and mortality worldwide, mainly because men are more likely to risk their health and disregard preventative measures. One potential explanation for this pattern of results is that women tend to have more compassionate attitudes and show higher dislike than men for others' suffering (Atari et al., 2020; Luoto and Varella, 2021). Women also tend to be higher than men in COVID-19-related disgust, as well as general risk aversion and neuroticism (Luoto and Varella, 2021).

These findings present an additional puzzle for evolutionary explanations of unrealistic optimism. Specifically, why do those more likely to experience an adverse outcome tend to underestimate their risk relative to those less likely? While there

are a number of possible answers to this question, we discuss two here. First, considering this question within the EMT framework, it is possible that the costs of risk aversion are higher for those with a greater risk compared to a lesser risk in certain situations (Haselton and Buss, 2000). Specifically, the opportunity costs associated with pessimism might disproportionately affect those at higher risk if the conflict between avoiding risk and achieving other fitness-relevant goals is particularly strong for these individuals. For example, young adults (males in particular) often discount their risk of sexually transmitted infections (STIs) to a greater extent than older adults, despite being at a much higher risk (Ethier et al., 2003; Wolfers et al., 2011; Syme et al., 2017). This may be because the benefits of mating success, which are on average higher for younger adults than older adults, overshadow the costs associated with STIs. Such conflicts between adaptive domains (in this case, mating success and disease avoidance) constitute an adaptive metaproblem (Al-Shawaf, 2016; Rantala et al., 2019; Varella et al., 2021).

A second, related possibility is that high-risk individuals have a greater need for the aforementioned psychological benefits related to unrealistic optimism than low-risk individuals. That is, unrealistically optimistic beliefs may help those at an especially high risk for adverse events cope with the reality of their situation (Taylor and Brown, 1994; McKay, 2009; Makridakis and Moleskis, 2015). For example, with COVID-19 risk, in the absence of any optimistic buffer, those with a higher risk for morbidity and mortality would be expected to experience a great deal of distress compared to those with a lower risk. In addition to bearing psychological costs, such distress may also prevent high-risk individuals from meeting key affiliative (and other fitness-relevant) goals that are especially salient under threat (Dezecache et al., 2020; Varella et al., 2021). This conflict between affiliative needs and disease avoidance can, again, be thought of as representing an adaptive metaproblem (Al-Shawaf, 2016; Rantala et al., 2019; Varella et al., 2021). Furthermore, high-risk individuals may also be employing a "free-riding" strategy, enjoying the safety benefits of others' cautiousness while not adjusting their behavior commensurate with their high risk for morbidity and mortality (Yong and Choy, 2021). In doing so, these individuals might be able to achieve other fitness goals without drastically increasing their already elevated risk.

Unrealistic Optimism and the COVID-19 Pandemic

While these insights may help to explain how natural selection could favor optimism biases, particularly in high-risk individuals, it is still unclear why unrealistic optimism would operate in contexts where it almost certainly increases the likelihood of serious adverse outcomes. One possibility is that unrealistic optimism leads to maladaptive outcomes, especially when individuals are faced with types (or scales) of risk that were not present in ancestral environments. For example, facing risk of cardiovascular disease—and being presented with knowledge about how to prevent it—is an evolutionarily novel situation. Accordingly, individuals may be poorly equipped to effectively weigh the costs (e.g., managing diet, exercising, etc.) and benefits (reduced odds of mortality) of taking steps to mitigate the risk of heart attacks and strokes, events that may not occur for many years into the future.

Although infectious diseases have been a threat throughout human history, the extremely high population density and international mobility that allowed the current large-scale pandemic to develop are novel. Accordingly, individuals may be unrealistically optimistic about their likelihood of infection from the SARS-CoV-2 virus or severe illness from COVID-19 disease, translating to dire consequences for those with high risk of infection, morbidity, and mortality worldwide. For example, the 2005 H5N1 avian influenza outbreak was a major public health challenge in many Asian, European, and African countries (de Zwart et al., 2007). Although this outbreak never reached pandemic levels, the highly pathogenic nature of this virus was significant (Peiris et al., 2007). In Hong Kong, where risk of exposure was elevated relative to many other countries, local residents perceived only moderate risk from buying live poultry. Specifically, only 36% of respondents in one survey agreed that purchasing live chickens was risky, and over 78% of households reported buying them during the peak of the epidemic in Asia (Fielding et al., 2005).

Moreover, while the personal health problems associated with COVID-19 are imminent, some people have still not experienced negative outcomes related to COVID-19 (or any other serious infectious disease outbreak) first-hand. In this way, the consequences of COVID-19 may seem, for some, distant in space in such a way that they do not perceive it as a significant threat. This may lead to them underestimating the risk of becoming infected or developing severe symptoms in general, tipping the scale toward unrealistic optimism and reducing investment in behaviors to reduce risk. In such a fashion, there was a false sense of security in certain countries and regions during the original SARS-CoV-1 epidemic (de Zwart et al., 2007). Education in the United States and Canada about the risks of SARS-CoV-1 virus was relatively unsuccessful at a large scale, as most of the populations remained unaware of the potential impacts of the virus (Blendon et al., 2004), in part because of its low level of spread (Blendon et al., 2004), and despite the fact that the United States and Canada experienced significant economic damage. In contrast, those in the Netherlands reported high levels of awareness for the SARS-CoV-1 virus (Brug et al., 2004). Although high perceptions of risk may have caused more worry, individuals also reported taking additional precautions to avoid the virus (Brug et al., 2004).

Current Aims

The purpose of the present project was to examine relationships among personal risk for severe COVID-19 disease, risk perceptions, and preventative behaviors in a large community cohort. It was predicted that those with higher clinical risk of severe COVID-19 disease (as determined by self-reported pre-existing conditions, demographic factors, and clinical characteristics) would exhibit unrealistic optimism and behave in ways inconsistent with their elevated risk of morbidity and mortality. Consistent with previous research on unrealistic optimism (Weinstein, 1982; Reyes-Velázquez and

Sealey-Potts, 2015; Shepperd et al., 2015; Jefferson et al., 2017), we predicted that this positive illusion may partially buffer high-risk individuals from the psychological consequences of the current pandemic. However, supporting the hypothesis that unrealistic optimism may lead to maladaptive outcomes when individuals face evolutionarily novel threats, we predicted that individuals with a higher risk of developing severe COVID-19 disease would not take more precautions than those with a lower risk.

METHODS

Overview and Study Design

Data analyzed for the present study were collected as part of the Waco COVID Survey, a serological surveillance project of SARS-CoV-2 virus in McLennan County, Texas, United States. McLennan County comprises ∼1,000 square miles in Central Texas, with a 2019 population estimate of 256,600 individuals with 27% Hispanic or Latina/Latino and 14.8% African American, 14.7% age 65 and above, 24.2% with a Bachelor degree or higher, 18% living below the national poverty line, and 18.4% without health insurance (while under the age of 65) (http://co.mclennan.tx.us/; https://www.census.gov/quickfacts/mclennancountytexas).

The primary purpose of this larger study was to prospectively determine the incidence of SARS-CoV-2 virus infection in several hundred asymptomatic individuals over the course of 4 months following the relaxation of shelter-in-place orders (shelter-in-place began on March 13th in Texas, with non-essential businesses opening back up on May 1st, 18th, and 22nd). This project was based on a repeated sampling protocol of targeted (non-random) clusters of individuals (all asymptomatic) that varied by exposure risk: those working in healthcare (including first responders), essential service employees (e.g., gas station attendants, lawn maintenance workers, grocery store employees, restaurant workers involved in food preparation for home delivery services or carry-out), employees in businesses and other organizations that reopened in May (e.g., restaurants, movie theaters, churches), and those who had claimed to strictly follow shelter-in-place and all public health recommendations. None of the participants included in the present analysis tested positive for IgG antibody against the SARS-CoV-2 virus (using EUROIMMUN COVID-19 ELISA with emergency use authorization).

Recruitment took place via Facebook, Twitter, and the Waco Tribune-Herald newspaper. Participation was limited to residents of McLennan County, Texas (since December 2019), age 18 years or older, fluency in English or Spanish (all materials were available in both languages), and absence of any signs or symptoms of COVID-19 disease, including cough, shortness of breath or difficulty breathing, pain or pressure in the chest, body temperature at or above 100 degrees Fahrenheit (37.8 degrees Celsius), chills, repeated shaking, sore throat, temporary loss of taste or smell, persistent headache, inability to stay awake, recent confusion, blush lips or face, muscle pain, vomiting, nausea, or diarrhea. Potential participants registered on a HIPAA-compliant website and then completed an extensive online questionnaire before visiting the Madison Cooper Community Clinic of Waco Family Medicine for anthropometric measurements and a venous blood draw. Participants made repeated visits monthly for venous blood draws to determine anti-SARS-CoV-2 IgG antibody levels and complete blood count. The data in the present analysis include those collected in the initial intake questionnaire.

The questionnaire included 103 questions (mostly multi-part each; ∼30 min in length) about demographics, education, socioeconomic status, household composition (and health status of household members), religiosity, political leniency, occupation history, use of personal protective equipment, hygiene, compliance with shelter-in-place orders, use of face coverings, social distancing, travel, changes in behavior since the pandemic began, current and past health, medication usage, any pre-existing conditions, knowledge and attitudes regarding the SARS-CoV-2 virus and COVID-19 disease, diet, alcohol consumption, activity levels, sleep, general risk avoidance, mental health and stress, and general affect, among other questions. Specific questions used in the present analysis (besides demographics) are listed below.

In response to the public health emergency of the SARS-CoV-2 pandemic, this project functioned as a public health surveillance activity, approved, and endorsed by the Waco-McLennan County Public Health District. As such, this project met exclusion criteria for institutional review board approval at 45 CFR 46.102(e) and (l) for Baylor University researchers, staff, and volunteers. Participation of Waco Family Medicine researchers, staff, and volunteers for the present project was approved by the institutional review board at Ascension Providence Hospital and Medical Center of Waco, Texas.

Materials

Clinical Risk Score for Severe COVID-19

In order to estimate each participant's approximate risk for severe COVID-19 disease, risk scores were calculated using information about demographic characteristics and pre-existing conditions previously shown to increase the odds of experiencing severe disease (CDC, 2020; Chidambaram et al., 2020; Petrilli et al., 2020). These included sex, smoking status, age, race/ethnicity, body mass index (BMI), and whether the participant reported ever being diagnosed with diabetes, cardiovascular disease, chronic obstructive pulmonary disease (COPD), kidney disease, liver disease, or cancer. Consistent with previous research examining how these factors contribute to COVID-19 outcomes (Petrilli et al., 2020), categorical variables were computed for age (19–44, 45–54, 55–64, 65–74, and >74 years old), and BMI (<25, 25–29.99, 30–39.99, >39.99).

Following methods used to develop clinical risk scores for other diseases and adverse medical events (Fong et al., 1999; Mehran et al., 2004; Sullivan et al., 2004; Callery et al., 2013; Zheutlin et al., 2019), each factor was weighted based on the strength of its association with severe COVID-19 disease found in previous studies. Specifically, weights were odds ratios (adjusted) for the effects of each factor derived from the results of logistic regression analyses reported in recently published meta-analyses and cohort studies (Chidambaram et al., 2020;

Petrilli et al., 2020)[1]. Reference groups for each factor (e.g., those without diabetes, cardiovascular disease, etc.) were assigned a weight of 1. These weights were summed and divided by eleven (the number of factors included in the score), with higher quotients representing a greater estimated susceptibility to severe COVID-19 disease outcomes. For example:

$$Clinical\ risk\ score = \frac{condition1^{*}odds\ ratio\ + condition2^{*}odds\ ratio \ldots + condition11^{*}odds\ ratio}{11}$$

COVID-19 Threat Appraisal

To assess the extent to which participants believed they were vulnerable to COVID-19 disease, questions were asked about their perceived likelihood of becoming infected by the SARS-CoV-2 virus and, if infected, their likelihood of experiencing severe COVID-19 disease. Specifically, participants responded to the questions: "What do you consider to be your own probability of getting infected with COVID-19?" and "How severe would contracting COVID-19 be for you (how seriously ill do you think you will be)?" Participants responded using 7-point Likert-type scale (1 = very low; 7 = very high). A third question was also answered using the same scale: "How would you rate your knowledge level on how to prevent spread of COVID-19?" This latter item was included to control for participants' perceived knowledge about SARS-CoV-2 virus transmission when examining perceptions of risk.

Self-Isolation During Shelter-in-Place Order and Travel

Participants were asked about the frequency at which they left their homes during the Texas shelter-in-place order (March 13 through May 1, 2020). They were further asked approximately how many times in an average week they left their homes during that period for the following reasons: buying essential supplies (e.g., groceries or water), going to a friend's house, going to a gas station, going to a liquor store, picking up food from a restaurant, and going to a public park. Participants responded with a whole number for each activity.

Participants were also asked about their travel following March 13, 2020, providing information about dates and locations for all travel outside of their city of residence (up to five trips). The total number of trips made within Texas and outside of Texas were calculated separately. The latter number included both out of state and out of country travel, as only five participants reported trips outside of the United States following March 13.

Psychological Distress During the Pandemic

Participants completed three measures to estimate psychological distress during the pandemic. First, participants were asked to rate their agreement with two statements: "COVID-19 makes me feel helpless" and "COVID-19 makes me depressed" using 7-point Likert-type scale (1 = strongly disagree; 7 = strongly agree). Second, participants completed the short-form Perceived Stress Scale (PSS-4) (Herrero and Meneses, 2006). This scale assesses the frequency at which participants feel stressed and overwhelmed in the month prior to their participation date ($\alpha = 0.80$).

Covariates

The following additional variables that may covary with perceived or actual COVID-19 risk, social distancing behavior and travel, and/or psychological distress during the pandemic were included in the analyses (see **Tables 1–3** for additional details about these variables): general risk tolerance (i.e., "Are you generally someone who tends to take risks, or do you tend to avoid risks?"), education, self-rated knowledge about COVID-19, whether or not the participant had health insurance, number of cohabitants in households, whether or not the participant worked as a healthcare provider or first responder, average daily encounters with a co-worker or friend/family member within six feet without a face covering[2], and whether the participant: (a) knew someone who had been diagnosed with COVID-19, (b) knew someone who had been hospitalized with COVID-19, (c) knew someone who died from COVID-19, (d) provided care for a COVID-19 patient, and (e) had been within six feet of someone who had been diagnosed with COVID-19.

Data Analysis Plan

Descriptive statistics are displayed in **Tables 2–3**. All analyses were conducted using SPSS (v27) and MPlus (v8) statistical software. All p values were two-tailed and considered significant at the level $p < 0.05$. First, variables were examined for normality and the presence of outliers (i.e., three standard deviations above or below the mean). Data for frequency of travel and leaving home during the shelter-in-place order, as well as the risk score, were positively skewed. Accordingly, model parameters were estimated using robust maximum likelihood estimation in MPlus, an estimation method that is robust to non-normality (Yuan and Bentler, 2000). Additionally, data for 70 participants contained outliers for at least one variable. Models were tested both with and without these outlying data points included; any changes in the pattern or significance of results across these models are noted in the "Results" section (see also **Table 4**).

To examine the relationship between estimated risk for severe COVID-19 disease and the outcomes of perceived risk, behavior during the shelter-in-place order, and psychological distress, we simultaneously regressed each dependent variable on risk scores in a multivariate model. The variables measuring the frequency of

[1]Odds ratios for sex, smoking status, diabetes, cardiovascular disease, COPD, kidney disease, liver disease, and cancer were obtained from Chidambaram et al., 2020 (**Table 1**). Odds ratios for age, race/ethnicity, and BMI were obtained from Petrilli et al., 2020 (**Table 3**).

[2]Mean composite ($\alpha = 0.78$) of average number of encounters each day with (a) friend/family member prior to March 13, (b) co-worker prior to March 13, (c) friend/family member between May 1 and May 18th/22nd, (d) co-worker between May 1 and May 18th/22nd, (e) friend/family member after May 18th/22nd, and (f) co-worker after May 18th/22nd.

TABLE 1 | Basic demographic statistics.

Characteristic	*N* (%)	Mean (*SD*)	Median (range)
Total	492 (100)		
Age	492 (100)	44.4 (14.25)	42 (19–87)
Group			
3	*180 (36.6)*		
4	*108 (22.0)*		
5	*100 (20.3)*		
6	*88 (17.9)*		
7	*16 (3.3)*		
Sex/Gender			
Female	309 *(62.8)*		
Male	183 *(37.2)*		
Racial identification			
American Indian or Alaskan Native	*1 (0.2)*		
Asian	6 *(1.2)*		
Black/American Indian	*12 (2.4)*		
Native Hawaiian or other Pacific Islander	*1 (0.2)*		
White	*430 (87.4)*		
More than one race	*31 (6.3)*		
Other/Missing	*11 (2.2)*		
Hispanic, Latino, or of Spanish origin			
Yes	*96 (19.5)*		
No	*395 (80.3)*		
Currently employed			
Yes	*413 (83.9)*		
No	*79 (16.1)*		
Worked as healthcare provider or a first responder since December 2019			
Yes	*177 (36.0)*		
No	*314 (63.8)*		
Currently have health insurance			
Yes	*460 (93.5)*		
No	*32 (6.5)*		
Type of insurance			
Medicare	*44 (8.9)*		
Private	*417 (84.6)*		
Other/Missing	*32 (6.5)*		
Highest level of education			
No high school or GED	*1 (0.2)*		
High school/GED	*12 (2.4)*		
Some college	*71 (14.4)*		
2-year degree (associate's)	*67 (13.6)*		
Professional certification	*31 (6.3)*		
4-year college degree	*136 (27.6)*		
Some grad school, no degree	*28 (5.7)*		
Master's degree	*91 (18.5)*		
Doctoral degree	*51 (10.4)*		
Other graduate degree	*4 (0.8)*		
Cohabitants in household	492 (100)	2.2 (1.63)	2 (0–10)
Childhood SES–partial	492 (100)	3.8 (1.52)	3.7 (1–7)
Political affiliation			
Democrat or lean democrat	*133 (27.0)*		
No lean	*137 (27.8)*		
Republican or lean republican	*219 (44.5)*		

TABLE 2 | Health descriptive statistics.

Characteristic	*N* (%)	Mean (*SD*)	Median (range)
BMI	492 (100)	29 (6.42)	28.1 (16.1–56.5)
Chronic infectious diseases			
Yes	*4 (0.8)*		
No	*488 (99.2)*		
Chronic non-infectious diseases or medical conditions			
Yes	*216 (43.9)*		
No	*271 (55.1)*		
COVID-19 disease related pre-existing conditions (≥1)			
Yes	*205 (41.7)*		
No	*287 (58.3)*		
Specific COVID-19 disease related pre-existing conditions (self-reported)			
Age >65	*48 (9.8)*		
Any cardiovascular/heart condition, including COPD, congestive heart failure, and hypertension	*58 (11.8)*		
COPD	*1 (0.2)*		
Any chronic lung disease, including moderate or severe asthma	*27 (5.5)*		
Chronic kidney disease	*3 (0.6)*		
Liver disease	*2 (0.4)*		
Diabetes	*19 (3.9)*		
Obesity	*98 (19.9)*		
Having an immune deficiency, including HIV	*3 (0.6)*		
Receiving cancer treatment or other immune weakening medications including corticosteroids	*3 (0.6)*		
Smoking or vaping	*36 (7.3)*		
Living in a nursing home or long-term care facility	*0 (0.0)*		
Influenza vaccine since September 2019			
Yes	*336 (68.8)*		
No	*156 (31.7)*		
Smoking and vaping			
Smoking	*29 (5.9)*		
Cigarettes per day		*10 (5.74)*	*10 (0–30)*
Vaping	*10 (2.0)*		
Puffs per day		*72 (91.74)*	*26.5 (12–300)*
Neither	*452 (91.9)*		
Smokeless tobacco or nicotine products use			
Yes	*19 (3.9)*		
No	*473 (96.1)*		
Hours per week spend on physical exercise	**491 (99.8)**	**7.7 (24.43)**	**4 (0–500)**
Diet			
On a diet	103 (20.9)		
No special diet	373 (75.8)		
COVID-19 disease risk score	492 (100)	1.1 (0.1)	1 (1–1.7)

travel outside of participants' home city were modeled as count data (with a high frequency of zeroes) and parameter estimates were generated using negative binomial regression (Gardner

TABLE 3 | Exposure, risk behavior, and risk perception.

Characteristic	*N* (%)	Mean (*SD*)	Median (range)
Contact within 6 feet per day with			
Coworker or client/patron before March 13th	*467 (94.9)*	*22.5 (38.21)*	*10 (0–500)*
Friend or family member before March 13th	*465 (94.5)*	*13.8 (21.54)*	*8 (0–203)*
Coworker or client/patron between May 1st and May 18th/22nd	*467 (94.9)*	*6.6 (16.31)*	*1 (0–200)*
Friend or family member between May 1st and May 18th/22nd	*466 (94.7)*	*10.8 (20.58)*	*5 (0–200)*
Coworker or client/patron after May 18th/22nd	*467 (94.9)*	*5.9 (15.64)*	*1 (0–200)*
Friend or family member after May 18th/22nd	*466 (94.7)*	*10.4 (20.54)*	*4 (0–200)*
Exposure to			
Animal with confirmed or suspected COVID-19 disease			
Yes	*10 (2.0)*		
No	*481 (97.8)*		
Know someone who has been diagnosed with COVID-19 disease			
Yes	*335 (68.1)*		
No	*157 (31.9)*		
Know someone who has been hospitalized from COVID-19 disease			
Yes	*140 (28.5)*		
No	*352 (71.5)*		
Know someone who has passed away from COVID-19 disease			
Yes	*81 (16.5)*		
No	*410 (83.3)*		
Provide a care for a COVID-19 disease patient			
Yes	*88 (17.9)*		
No	*403 (81.9)*		
Be within 6 feet of anyone that has been diagnosed with COVID-19 disease			
Yes	*146 (29.7)*		
No	*346 (70.3)*		
Wash hands with soap and water or use sanitizer			
Before the pandemic	*491 (99.8)*	*9.9 (10.57)*	*6 (0–100)*
Since the pandemic	*491 (99.8)*	*17.5 (15.07)*	*12 (1–100)*
Change before-after	*491 (99.8)*	*7.6 (9.06)*	*5 (−15–97)*
Left home between March 13th and May 1st			
To buy essential supplies	*491 (99.8)*	*2.8 (4.78)*	*2 (0–60)*
To a friend's house	*488 (99.2)*	*0.7 (2.95)*	*0 (0–60)*
To a gas station	*491 (99.8)*	*1.9 (3.01)*	*1 (0–42)*
To a liquor store	*486 (98.8)*	*0.3 (0.84)*	*0 (0–10)*
Pick up food from a restaurant	*488 (99.2)*	*2.8 (4.53)*	*2 (0–56)*
To a public park	*490 (99.6)*	*1.2 (3.68)*	*0 (0–60)*
Times traveled within Texas after March 13	492 (100)	0.9 (1.3)	0.5 (0–5)
Times traveled outside of Texas after March 13	492 (100)	0.2 (0.5)	0.0 (0–3)
Self-rated knowledge level on how to prevent spread of SARS-CoV-2 virus	490 (99.6)	6.1 (0.95)	6 (1–7)
Self-rated probability of getting infected with SARS-CoV-2 virus	489 (99.4)	4.1 (1.59)	4 (1–7)
Self-rated severity of contracting COVID-19 disease	489 (99.4)	3.6 (1.52)	4 (1–7)
Self-rated adherence to recommendations from authorities in the country to prevent spread of SARS-CoV-2 virus	490 (99.6)	7 (1.67)	8 (1–8)
Willingness to take a vaccine if available	491 (99.8)	5.5 (1.98)	6 (1–7)
Willingness to live up to restrictions, even if not formal anymore, if there is a surge in cases of COVID-19	491 (99.8)	5.5 (1.64)	6 (1–7)
Self-reported feeling helpless because of COVID-19 disease	490 (99.6)	3.9 (2.26)	4 (1–8)
Self-reported feeling depressed because of COVID-19 disease	490 (99.6)	3.8 (2.3)	4 (1–8)
Tend to take risk	491 (99.8)	3.6 (1.74)	4 (1–7)
Perceived Vulnerability to Disease Perceived Infectability subscale (PVD-DP)-partial	492 (100)	3.1 (1.26)	3 (1–7)
Perceived Vulnerability to Disease Germ Aversion subscale (PVD-DP)-partial	492 (100)	5.1 (1.14)	5 (1.3–7)
Perceived stress scale-partial	492 (100)	2.4 (0.73)	2.3 (1–4.8)
Three domains of disgust scale-partial	491 (99.8)	4.6 (1.34)	4.7 (1–7)

TABLE 4 | Results of statistical models.

Dependent variable	Unstandardized beta coefficient (*SE*)		
	Primary model	Covariates included	Outliers removed
Risk perception			
Likelihood of infection	−2.63 (0.84)**	−1.80 (0.87)*	−2.93 (0.97)**
Likelihood of severe illness if infected	3.79 (0.64)***	3.38 (0.70)***	4.10 (0.95)***
Behavior during shelter-in-place order			
Buy supplies	−0.48 (2.19)	−0.50 (2.28)	0.11 (1.19)
Visit friend	7.14 (6.74)	7.25 (6.87)	−0.20 (0.87)
Gas station	−1.74 (1.11)	−1.50 (1.12)	−0.71 (1.24)
Liquor store	0.16 (0.48)	0.25 (0.47)	0.001 (0.35)
Pick up food from restaurant	−3.92 (1.67)*	−4.12 (1.73)*	−2.57 (1.87)
Public park	−1.85 (0.82)*	−2.07 (0.85)*	−1.78 (1.46)
Travel during pandemic			
Within State	1.83 (0.57)**	1.84 (0.58)**	1.71 (0.70)*
Outside of State	−0.98 (0.94)	−1.43 (0.99)	−1.01 (1.98)
Psychological distress during pandemic			
Perceived stress	−1.21 (0.32)***	−1.17 (0.34)**	−1.26 (0.49)*
Feelings of depression	−3.37 (1.04)**	−4.27 (1.09)***	−3.28 (1.44)*
Feelings of helplessness	−3.60 (1.09)**	−5.27 (1.12)***	−3.72 (1.50)*

*SE, standard error. *p < 0.05, **p < 0.01, ***p < 0.001.*

TABLE 5 | Spearman rank correlations between COVID-19 disease risk score and covariates.

Variable	1	2	3	4	5	6	7	8	9	10	11	12
1. COVID-19 disease severity risk score	-											
2. Risk tolerance	−0.02	-										
3. Education	−0.07	0.03	-									
4. Self-rated knowledge about COVID-19 disease	0.02	−0.03	0.14***	-								
5. Has health insurance	0.06	−0.03	0.14***	0.03	-							
6. Number of cohabitants	−0.27***	0.04	−0.04	−0.10*	0.01	-						
7. Healthcare worker or first responder	−0.19***	0.03	−0.03	0.18***	0.06	0.07	-					
8. Interactions without face coverings	−0.11*	0.19***	−0.09*	−0.09*	−0.03	0.26***	0.11*	-				
9. Know someone diagnosed with COVID-19 disease	0.03	−0.02	−0.01	−0.03	0.01	−0.01	0.01	−0.04	-			
10. Know someone hospitalized with COVID-19 disease	0.08	0.06	0.10*	0.03	−0.09*	−0.04	−0.004	−0.03	0.39***	-		
11. Know someone who died from COVID-19 disease	0.07	−0.08	0.004	0.07	−0.07	−0.02	0.05	−0.08	0.22***	0.49***	-	
12. Provided care for someone with COVID-19 disease	−0.17***	0.03	0.05	0.20***	0.06	−0.01	0.49***	0.07	0.15***	0.11*	0.08	-
13. Within six feet of someone with COVID-19 disease	−0.10*	0.11*	−0.05	0.15***	−0.03	−0.04	0.26***	0.09	0.27***	0.19***	0.13**	0.65***

**p < 0.05, **p < 0.01, ***p < 0.001.*

et al., 1995). Because the variables assessing the average number of times participants left their home (but stayed within the city) included non-integers (e.g., 0.5 times per week on average), these data were not modeled as count data (i.e., standard linear regression parameter estimation was used). This model was tested a second time controlling for covariates (see above for full list). Zero-order correlations between the estimated COVID-19 severity risk score and all covariates are displayed in **Table 5**. Given the non-normality of the risk measure, Spearman rank-order correlation procedure was used to estimate coefficients and significance values.

RESULTS

Characteristics of the sample are shown in **Table 1**. A total of 495 participants completed the behavioral survey (women: 311, men: 183, other: 1, $M_{age} = 44.43$, $SD_{age} = 14.28$). Three participants provided incomplete data for the variables needed to calculate the risk score and were thus excluded from analyses.

COVID-19 Threat Appraisal

Unstandardized beta coefficients and standard errors for parameters in all models are displayed in **Table 4**. Results of the regression analysis revealed that as participants' clinical risk score for severe COVID-19 disease increased, their perceived risk of experiencing severe illness if infected also increased ($b = 3.79$, $SE = 0.64$, $t = 5.96$, $p < 0.001$). In contrast, higher clinical risk scores for severe COVID-19 disease predicted lower perceived risk of becoming infected with SARS-CoV-2 virus ($b = -2.63$, $SE = 0.84$, $t = -3.12$, $p = 0.002$). In other words, while individuals with a high clinical risk score seemed to acknowledge their elevated likelihood of experiencing severe COVID-19 if infected, they actually reported lower perceived risk of becoming infected in the first place. Removing outliers did not change the pattern or significance of these results (likelihood of severe illness: $p < 0.001$; likelihood of infection: $p = 0.002$), nor did controlling for covariates (likelihood of severe illness: $p < 0.001$; likelihood of infection: $p = 0.037$).

Self-Isolation During the Shelter-in-Place Order and Travel

Regarding travel within the participants' city of residence during the shelter-in-place order, higher clinical risk scores for severe COVID-19 disease predicted a lower frequency of going to a park ($b = -1.85$, $SE = 0.82$, $t = -2.27$, $p = 0.023$) and picking up food from a restaurant ($b = -3.29$, $SE = 1.67$, $t = -2.35$, $p = 0.019$). However, clinical risk scores were not significantly related to frequency of leaving the home to purchase supplies ($b = -0.48$, $SE = 2.19$ $t = -0.22$, $p = 0.825$), visiting a friend ($b = 7.14$, $SE = 6.74$, $t = 1.06$, $p = 0.299$), going to a gas station ($b = -1.74$, $SE = 1.11$, $t = -1.57$, $p = 0.118$), or going to a liquor store ($b = 0.16$, $SE = 0.48$, $t = 0.33$, $p = 0.741$).

While these results did not change when controlling for covariates (park: $p = 0.015$, restaurant: $p = 0.017$, supplies: $p = 0.827$, friend: $p = 0.291$, gas station: $p = 0.182$, liquor store: $p = 0.598$), all effects—including going to a park or restaurant—became non-significant when outliers were removed (park: $p = 0.222$, restaurant: $p = 0.170$, supplies: $p = 0.930$, friend: $p = 0.822$, gas station: $p = 0.567$, liquor store: $p = 0.999$). The change in statistical significance that occurred after outlying values were excluded may indicate that participants who reported very high frequencies of these activities did so in error. Specifically, it is possible that certain participants reported the total number of times they engaged in each activity between March 13 and May 1 instead of the average number of times per week.

While higher clinical risk scores did not significantly predict frequency of travel outside of the state of Texas ($b = -0.98$, $SE = 0.94$, $t = -1.04$, $p = 0.299$), those with higher scores reported a greater number of trips within Texas than those with lower scores ($b = 1.83$, $SE = 0.57$, $t = 3.20$, $p = 0.001$). The pattern and significance of these results did not change when controlling for covariates (outside of state: $p = 0.145$; within state: $p = 0.001$), nor did they change when outliers were excluded (outside of state: $p = 0.609$; within state: $p = 0.015$).

In sum, these findings suggest that individuals at a high risk for severe COVID-19 do not generally behave differently than those at low risk. Specifically, clinical risk scores were not reliably associated with participants' frequency of leaving their homes during the shelter-in-place order, nor were they related to out-of-state travel. Unexpectedly, participants with higher clinical risk scores actually reported traveling more often outside of their resident city, but within their home state of Texas, than those with lower risk scores.

Psychological Distress During the Pandemic

Higher clinical risk scores for severe COVID-19 disease were associated with lower perceived stress (i.e., PSS-4 scale) ($b = -1.21$, $SE = 0.32$, $t = -3.79$, $p < 0.001$), feeling less depressed by the pandemic ($b = -3.37$, $SE = 1.042$, $t = -3.24$, $p = 0.001$), and feeling less helpless in response to the pandemic ($b = -3.60$, $SE = 1.09$, $t = -3.31$, $p = 0.001$). In other words, despite their increased likelihood of severe COVID-19 if infected, individuals with higher clinical risk scores appear to experience less psychological distress than those with lower scores. The pattern and significance of these results did not change when controlling for covariates (stress: $p = 0.001$; depressed: $p < 0.001$; helpless: $p < 0.001$), nor did they change when outliers were removed (stress: $p = 0.010$; depressed: $p = 0.023$; helpless: $p = 0.013$).

DISCUSSION

Evolution, Unrealistic Optimism, and COVID-19

Unrealistic optimism is a common human feature. Despite posing the potential cost of promoting risky behavior in the face of uncertain outcomes (Weinstein, 1982; Michailova and Schmidt, 2016; Karl et al., 2020), unrealistic optimism may also provide a number of psychological and health benefits (Johnson and Fowler, 2011; Kleiman et al., 2017; Rozanski et al., 2019). The decreased worry associated with unrealistic optimism

may improve mental well-being of some individuals during the COVID-19 pandemic, which is associated with mental health and sleep disturbances (Pappa et al., 2020; Pfefferbaum and North, 2020), and overconfidence may increase productivity through increasing morale and persistence (Johnson and Fowler, 2011). It is also possible that overconfidence may decrease productivity by setting unrealistic goals and failing which can lead to psychological and financial struggles (Makridakis and Moleskis, 2015). Given the possible benefits of overconfidence, it has been proposed that positively-biased affect, beliefs, and attitudes were favored by natural selection (Johnson and Fowler, 2011). In line with this hypothesis, behavior consistent with optimism biases have been observed in a variety of non-human animal species (Harding et al., 2004; Matheson et al., 2008).

Despite some hypothesized psychological benefits discussed above, unrealistic optimism can be dangerous due to improper assessment of hazardous situations, and inferring that optimism bias has evolutionary origins does not mean that unrealistic optimism is an "optimal" strategy in every situation. This is especially true when individuals are faced with a novel source (or scale) of risk that was not present in the environments under which optimism biases may have evolved. For example, unrealistic optimism about one's probability of becoming infected with the SARS-CoV-2 virus or of developing severe COVID-19 disease may be maladaptive, leading to behaviors that increase one's odds of exposure. This could be especially harmful for those with high risk of developing severe COVID-19 disease if infected. In the case of COVID-19, a disease with a high percentage of asymptomatic cases (Cheng et al., 2020; Huff and Singh, 2020), a long contagious period before showing symptoms (Tindale et al., 2020), it is possible that for some people it can be challenging to recognize the risk of becoming infected with the virus (Varella et al., 2021).

Age and comorbidities are strong indicators of hospital admission and, to a lesser degree, mortality among patients with COVID-19 disease (Petrilli et al., 2020). Men over the age of 65 and smokers are among the highest at risk for adverse outcomes of COVID-19 disease (Zheng et al., 2020). Other factors that may influence COVID-19 disease outcomes include comorbidities like hypertension, diabetes, respiratory diseases, or cardiovascular diseases (Albitar et al., 2020; Li et al., 2020; Zheng et al., 2020). More specifically, chronic obstructive pulmonary disease (COPD), cerebrovascular disease, and cardiovascular disease are associated with severe COVID-19 disease (Sole et al., 2020). People with cancer also experience higher severity of COVID-19 disease in conjunction with diagnostic and therapy delays (ElGohary et al., 2020). However, it must be noted that most, if not all, systematic reviews and meta-analyses at this time are skewed toward populations in China; thus, the exact risk resulting from a pre-existing condition may differ across populations.

While age and other comorbidities have been clearly linked to adverse outcomes of COVID-19 (Petrilli et al., 2020), many high-risk individuals continue to disregard public health guidelines and recommendations. Though concern for the novel coronavirus is persistent across borders, risk perception may also be culturally biased. For example, countries that abide by strict cultural norms reported almost five times fewer cases of COVID-19 and almost eight times lower number of deaths, suggesting a strong influence of this factor on recommendation compliance and risk perception (Gelfand et al., 2021). Additionally, factors such as personal experience, prosocial and individual values, trust in government (Dryhurst et al., 2020), life history strategy (Corpuz et al., 2020), and sex (Luoto and Varella, 2021) all influence risk perception. Individual differences in disease avoidance motivation also likely play important mediating or moderating roles in relationships between actual risk, perceived risk, and behavior (Makhanova and Shepherd, 2020). Future research is needed to examine how each of these factors influence the pattern of results found in the current research.

Risk perception correlates significantly with use of preventative health behaviors for COVID-19 in ten different countries (Dryhurst et al., 2020). In the United States, people reported a higher perceived risk of COVID-19 disease compared to other current health threats (Zhong et al., 2020). Despite this, many people still do not sufficiently understand SARS-CoV-2 virus transmission and COVID-19 disease prevention (Zhong et al., 2020). An individual's perception of their own risk to a threat impacts their health behaviors (Ferrer and Klein, 2015), and unrealistic optimism, especially among high-risk individuals, may be partly responsible for the avoidance of necessary preventative measures during the current pandemic (Dolinski et al., 2020). With the threat of the SARS-CoV-2 virus continually growing, understanding risk perception and subsequent behavioral outcomes regarding COVID-19 are essential to public health.

Perceived Risk and Compliance With State Law and Public Health Recommendations

The present project examined whether one's calculated clinical risk for severe COVID-19 disease (based on the aforementioned demographic and clinical characteristics) was related to risk perception, behavior, and psychological distress during the current pandemic. The data reveal that, while individuals with a higher clinical risk score accurately report greater perceived risk for severe illness, they actually perceive a lower risk of being infected with SARS-CoV-2 virus (relative to those with fewer or no pre-existing conditions). Although counterintuitive, the finding is consistent with the wide body of research on unrealistic optimism in the context of health risk management (Sharot et al., 2011; Shepperd et al., 2015; Jefferson et al., 2017). In particular, the current results provide further support for research demonstrating that unrealistic optimism about the likelihood of experiencing adverse health outcomes is greater for those with a higher number of risk factors (Karl et al., 2020). It must be noted here that not all studies support the cost-benefit basis of the evolution of unrealistic bias, and in some cases, it can be a potentially costly cognitive bias (Jefferson, 2017).

Within the present dataset, there is not reliable evidence that those at higher risk for severe COVID-19 disease traveled less during and after the shelter-in-place order (March 13 through May 1) than those with lower risk. That is, clinical risk scores for severe COVID-19 disease were not significantly related

to individuals' frequency of leaving their homes to engage in activities like visiting friends or going to the grocery store. While higher clinical risk for severe COVID-19 disease initially predicted fewer trips to the park and picking up food from restaurants, these effects were not statistically significant after outliers were removed. Moreover, results revealed that higher risk for severe COVID-19 disease was actually associated with more trips outside of the participants' resident city (but within the state). In other words, individuals with a higher number of pre-existing conditions did not appear to exercise more caution than those with fewer conditions, despite their elevated risk for morbidity and mortality from COVID-19. While these results may be surprising at face value, they lend further support for the prediction that those at a high risk for severe COVID-19 are unrealistically optimistic about their likelihood of infection. It is important to consider that if those at a high risk for severe COVID-19 disease are willing to break shelter-in-place orders and other public health recommendations, it is likely that other individuals without pre-existing conditions are also willing to disregard safety recommendations. Many people unfortunately choose to disregard public health recommendations during the current pandemic for various reasons (e.g., personal, social, political, etc.), and unrealistic optimism may be contributing to poor decision making in many of these individuals. On the other side, one study has found that islandic, Croatian men scored higher on perceptions of infectability during the COVID-19 pandemic than before, while women did not, and the authors hypothesize that it may reflect the objectively higher risk of COVID-19 (Hromatko et al., 2021). This seems to suggest that at least some amount of increased personal risk for infection is acknowledged by higher-risk individuals during the current pandemic.

Results of the present study also revealed that higher clinical risk scores are associated with less reported stress, and fewer feelings of depression and helplessness during the pandemic. One plausible explanation is that, in believing that they are less likely to contract the SARS-CoV-2 virus, individuals with higher risk for severe COVID-19 disease experience fewer negative emotions. While these results are consistent with research finding that unrealistic optimism acts as a psychological buffer from stress (Taylor et al., 1992; Taylor and Brown, 1994; Makridakis and Moleskis, 2015), that those with a higher disease risk actually reported less distress than those with a lower disease risk is unexpected. In other words, this pattern of results suggests that unrealistic optimism in the face of serious COVID-19 risk goes beyond merely assuaging negative emotions. Instead, distress may be suppressed by optimism to a level below even what those without pre-existing conditions report. Another possible explanation is that those with higher clinical risk scores are less likely to have experienced the distress associated with a friend or loved one developing severe COVID-19 disease. However, risk scores were not significantly related to whether or not participants knew someone who was hospitalized or passed away from COVID-19 disease (see **Table 5**).

It is worth noting that, within the present dataset, those at a higher risk for severe COVID-19 disease had smaller households and were less likely to report being a first responder/healthcare worker or to have cared for someone with COVID-19 disease (see **Table 5**). Higher clinical risk scores were also negatively correlated with the number of maskless interactions reported. It is therefore possible that, in this dataset, those with a higher risk for severe COVID-19 disease truly are less likely to become infected with the SARS-CoV-2 virus. In other words, do these individuals exhibit unrealistic optimism or do they realistically evaluate their risk of becoming infected? Although this cannot be determined definitively with the current cross-sectional data, there does not appear to be strong evidence for the latter possibility. Participants in this dataset with a higher disease risk score did not generally behave differently than those with a lower disease risk score during the shelter-in-place order, and they were actually more likely to travel outside of their resident city. Additionally, neither the pattern nor significance of the relationship between risk scores and perceived likelihood of infection changed after controlling for possible occupational exposure, number of cohabitants, and other factors that may influence infection probability. Nonetheless, it remains possible that an unmeasured covariate confounds the relationship between clinical risk scores and risk perception; this is a limitation of the current study.

Another potential limitation is that it is difficult to determine with the current data which risk factors for severe COVID-19, specifically, drive relationships between clinical risk scores and risk perceptions. In the present study, the three most common risk factors were age, male sex, and high BMI. However, each of these are likely to have unique effects on risk perception and behavior. For example, while one might be less mobile and risk averse in advanced age, male sex is conversely associated with greater engagement in risky behaviors during the pandemic, higher mobility, and lower adherence to preventative activities (Galasso et al., 2020; Luoto and Varella, 2021). Moreover, it is also difficult to discern which factor is driving COVID-19 risk, *per se*, because age is a common predictor of nearly all of the more potent risk factors, like diabetes, cardiovascular disease, etc. For this reason and others, it is important to exercise caution when thinking about cumulative risk in such a reductionist sense. That is, it is unlikely that one's total risk is truly just the sum of independent predictors. Accordingly, that we only apply an additive model of clinical risk without secondary validation in separate samples is a limitation of the current study. Future research using larger sample sizes might explore multiplicative and non-linear effects, as well as redundancy between risk factors. Meta-analyses are well-suited for this purpose.

A final limitation includes how unrealistic optimism was assessed. In the current study, risk perception was deemed unrealistic because those with higher clinical risk scores reported being less likely to become infected than those with lower scores, despite little evidence of this being true. It should be noted, however, that optimism biases are typically measured in a comparative fashion. That is, respondents are asked about their risk relative to others' (Weinstein, 1982; Ferrer et al., 2012; Shepperd et al., 2015). Future research is needed to determine whether a similar pattern of results would be found using a more commonly employed method of assessing unrealistic optimism.

Future Directions

The ecological fallacy prevents the results from the current dataset to be generalized to other populations within and outside of the United States. Almost 500 asymptomatic volunteers were selected from over 1,000 applicants of McLennan County, TX, residents based on the following self-reported risk factors: if they were a frontline worker or healthcare provider, if they were an essential employee, if they broke shelter-in-place orders to attend religious and other services/activities in person, or if they have followed all shelter-in-place and public health orders/recommendations. The dataset does not represent completely random selection from among the county residents and does not accurately reflect the percentage distribution of those above/below the poverty line (e.g., only 6.5% did not have health insurance) or minority status (e.g., only 19.5% of the dataset included Hispanic and Latina/Latino members). The dataset is also over-represented by individuals with above-average education who therefore likely have above-average concern about the current pandemic, although it is unlikely that differences in perceived risk are attributed to lack of education given the public health messaging about the current pandemic. However, the primary compensation from the present study was a free IgG antibody test for the SARS-CoV-2 virus, and those uninterested in knowing their serological status to the virus are less likely to be represented in the present dataset. Future work would ideally (but with great difficulty) include completely randomly selected community members resulting in a more diverse dataset.

One particularly interesting area for future research includes cross-cultural comparison of risk perception and its influence on preventative behaviors in relation to COVID-19 disease. Emerging infectious diseases (EIDs) have been a persistent global problem, and Asia has historically been an epicenter for many of these outbreaks. A considerable amount of effort has been put into surveillance and prevention in countries like India, where infectious disease outbreaks have been common (Mukherjee, 2017). In the United States and other high-income countries, the primary causes of mortality include non-communicable diseases (NCDs). Because of this trend, the United States healthcare infrastructure is primarily designed to manage the high prevalence of NCDs rather than EIDs. This may have exacerbated the lack of preparedness of the United States for the SARS-CoV-2 virus pandemic at the country, state, and individual levels (Katzmarzyk et al., 2020). Furthermore, cultural differences in tightness-looseness (Gelfand et al., 2021), as well as potential regional biological differences reflected in motivation to avoid infectious diseases (Skolnick and Dzokoto, 2013; Gassen et al., 2018; Cepon-Robins et al., 2021; Krams et al., 2021), may also influence certain countries' tendencies to invest heavily in pandemic preparedness.

In sum, the results of the current research provide partial evidence for a miscalibration between one's actual risk for severe COVID-19 disease, perceptions of risk, and behaviors that mitigate that risk. This study may lay the groundwork for future research to examine, in more detail, how unrealistically optimistic perceptions about infection likelihood and severity contribute to the spread of SARS-CoV-2 virus, particularly for those with pre-existing conditions.

DATA AVAILABILITY STATEMENT

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

DATA SHARING

De-identified data can be made available to researchers upon reasonable request.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Ascension Providence Hospital, Waco, TX. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

MM and EB conceived the Waco COVID Survey and implemented it with SW. MM wrote the survey, designed the study, and obtained the funding. EB designed and managed the websites. TN, JG, and MM managed the enrollment. JG and TN lead the data collection. MM and JG conceived the paper. TN and JG conducted the statistical analyses. AH contributed to data collection and manuscript preparation. JG, TN, AH, and MM wrote the manuscript.

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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.2021.647461/full#supplementary-material

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Extrinsic and Existential Mortality Risk in Reproductive Decision-Making: Examining the Effects of COVID-19 Experience and Climate Change Beliefs

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While the COVID-19 pandemic has presented an immediate risk to human life around the world, climate change poses an arguably greater—although less immediate—threat to our species' survival. Within the framework of life-history theory (LHT), this pre-registered study investigated whether extrinsic risk (i.e., external factors that pose a risk to an individual's life, e.g., COVID-19) and existential risk (i.e., risks with outcomes that threaten the existence of humans as a species, e.g., climate change) had similar or different relationships with reproductive decision-making. A UK representative sample of 325 participants between 18 and 35 years of age was asked to indicate their ideal number of children, ideal age to start having children, and whether their desire for a child had recently changed. Participants were asked about their experiences of COVID-19 and given a series of scales with which to assess their beliefs about climate change. In support of LHT, the study found evidence that knowing people who had been hospitalized with or died of COVID-19 was associated with a greater ideal number of children. Conversely, there was no clear evidence of a relationship between climate change beliefs and reproductive decision-making. The repercussions for understanding how we interpret and respond to different forms of mortality risk are discussed.

Keywords: mortality, life-history theory, existential risk, COVID-19, climate change

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INTRODUCTION

Typically, humans desire to have offspring. However, the psychological mechanisms that affect the desire to have children (and the number thereof) are still very much under debate (Sear et al., 2016). One of the more comprehensive approaches taken to addressing this question has been life history theory (LHT). Initially developed to explain between-species differences in reproductive rates, it has since been used to explain within-species variation in reproduction, behavior, and cognition (Scheiner, 1992; Ellis et al., 2009; Menie et al., 2021). LHT posits that because resources are finite, to maximize reproductive success, organisms must make trade-offs in resource allocation depending on the environment: Resources allocated to individual growth (whether physical, mental, or social) cannot also be allocated to the production of offspring

and vice versa (Scheiner, 1992; Sear, 2020). Put simply, if the environment is harsh or unstable, it is "best" to reproduce as soon as and as often as possible; however, if the environment is bountiful and stable, then growth should be prioritized.

Over the past 20 years, LHT has been increasingly applied to human behavior and has been used to understand the covariation in many human traits (Luoto et al., 2019a; Ellis et al., 2020; Sear, 2020). A key focus of this research has been to ascertain whether environmental factors trigger fast or slow life histories. That is, research has sought to determine how cues in the local environment that signal harshness and/or unpredictability trigger suites of present- or future-focused behaviors. Fast life-history strategies emphasize present-focused behavior, while slow strategies emphasize future-focused behavior (Nettle and Frankenhuis, 2019). While there is certainly evidence that heritability and genetics affect the development of life-history strategies (see Figueredo et al., 2006), research has often focused on socioeconomic status (SES), particularly but not exclusively during one's childhood. SES strongly impacts the quality of one's environment in general (Pepper and Nettle, 2017; Ellis et al., 2020), and SES is used as a proxy for a harsh environment (Griskevicius et al., 2011) and an environment of high morbidity and mortality (Ellis et al., 2009), while other measures have been used to measure environmental unpredictability in childhood (Young et al., 2020). The childhood environment is key to development (Figueredo et al., 2006), and researchers have suggested that cues of environmental quality in early childhood calibrate an individual's behavioral profile for what is likely a lifetime in that environment (Ellis et al., 2009, 2020; Del Giudice et al., 2015). Childhood SES has been associated with performance in future discounting tasks (Mittal and Griskevicius, 2014; cf., Ellis et al., 2020), personality development (Međedović, 2019), and reproductive decision-making (Griskevicius et al., 2011; Chipman and Morrison, 2015; Jaadla et al., 2020). Nevertheless, the potential for a large mismatch between an individual's current environment and their childhood environment means that human behavior should also be open to influence throughout one's life. Indeed, there is also ample evidence that the adult environment also adjusts behavior to a faster or slower approach to life (Quinlan, 2010; Nettle, 2017; Pepper and Nettle, 2017).

Extrinsic and Existential Risk

One direct and evolutionarily salient cue of a current harsh (or unstable; see Young et al., 2020) environment is death, or rather, a high local mortality rate. Extrinsic mortality risk, which is the risk of mortality over which one has no control, has been shown to increase the speed of one's life history across numerous domains, including reproductive decision-making (McAllister et al., 2016; Pepper and Nettle, 2017; André and Rousset, 2020). Importantly, such changes in response to extrinsic risk occur in response to the current local environment rather than to the childhood environment alone. For example, high local infant mortality has been associated with an earlier onset of reproduction (Quinlan, 2010), as has the number of bereavements an individual has experienced in the recent past (Pepper and Nettle, 2013). Thus, while childhood experiences likely determine general behavioral tendencies (Mittal and Griskevicius, 2014; cf., Wu et al., 2020), there is likely still plasticity in how one's life-history strategy calibrates to the current environment (Ellis et al., 2009; Nettle and Bateson, 2015; McAllister et al., 2016). We should expect that any sudden change in extrinsic risk, such as a global pandemic, might impact decision-making.

However, we as a species are unique in that we can comprehend, and cause, a very different type of risk—existential risk. Existential risk refers to threats that could cause human extinction or the permanent curtailing of human progress due to the destruction of the Earth's potential to sustain life (Bostrom, 2002; Cotton-Barratt and Ord, 2015; Schubert et al., 2019). Such threats could be natural (e.g., an asteroid colliding with Earth), but human technological progress has dramatically increased the threat of artificially inducing such an event (e.g., through rising temperatures as a result of burning fossil fuels). To quote E. O. Wilson, "the real problem of humanity is the following: we have paleolithic emotions; medieval institutions; and God-like technology."

It could be argued that existential risk is a form of extrinsic risk in that an existential risk is also a personally unavoidable risk to oneself and therefore to one's future offspring. Thus, the effects of an existential risk on life-history strategy might be no different than those of other cues that indicate potential future hardship (e.g., Wisman and Goldenberg, 2005; Griskevicius et al., 2011). However, by definition, we as a species have not experienced an existential threat (i.e., there are no day-to-day experiences that could act as an evolutionarily salient cue). Indeed, as the creation (e.g., mutually assured destruction) and comprehension (e.g., extraterrestrial objects) of such risks have depended on human technological progress, their evolutionary novelty potentially means they might produce unpredictable behavioral changes.

One example of an existential risk is climate change. While the firsthand effects of climate change are becoming apparent even in societies that have so far been insulated from them (Filkov et al., 2020; Parry et al., 2020), recent evidence suggests that such events are being conceptualized as local extrinsic risks to life rather than manifestations of existential risk (Schubert et al., 2019). Interestingly, while academic research on the psychological consequences of existential risk relevant to LHT is sparse (see Schneider-Mayerson and Leong, 2020), several recent polls have suggested that concerns regarding climate change are reducing the desire to have children (Miller, 2018; Relman and Hickey, 2019). The results of this polling data were recently supported by Schneider-Mayerson and Leong (2020); however, the results are at odds with the principles of LHT. If an individual fears greater future instability, should this fear not lead to a fast life history and a desire for more children now, while resources (at least in the West) are still plentiful? Indeed, with priming experiments demonstrating that imagining a harsh or unstable future leads to a faster life history (see McAllister et al., 2016), one would expect the same response in those that heed the warnings of climate scientists. As

stated, the evolutionary novelty of an existential risk might result in unexpected behavior changes due to the mismatch between current and ancestral conditions (see Li et al., 2018): Visible cues pointing to the precariousness of one's own mortality in the local environment might produce different behavioral responses when compared to more abstract concerns regarding future species-wide mortality due to large-scale ecological collapse (generated, for example, by exposure to media; see Brulle et al., 2012; Dunn et al., 2020).

The Current Study

The COVID-19 pandemic provides the opportunity to study both extrinsic and existential risks simultaneously. COVID-19 has increased the extrinsic mortality risk in Western, Educated, Industrialized, Rich, and Democratic (WEIRD) societies in a manner arguably not seen since the end of World War II. Therefore, it provides a novel opportunity to assess the impact of a sudden change in mortality risk on reproductive decision-making in a WEIRD population (i.e., the United Kingdom). It also allows for a comparison to be made between a sudden rise in extrinsic mortality risk and the existential risk posed by climate change. In doing so, it adds to the dearth of information regarding the effects of the latter.

The current study investigated whether experiences of COVID-19 and climate change beliefs impacted reproductive decision-making. Participants were asked to indicate their ideal number of children and the ideal age at which to have the first child. They were then explicitly asked whether their desire for a child or another child had increased or decreased during the pandemic. As stated in the pre-registration, it was predicted that COVID-19 experience (measured by illness experienced by the participant and their close associates and deaths of the latter) would predict an increase in the ideal number of children and a decrease in the ideal age of first birth. It was also predicted that COVID-19 experience would predict an increase in the immediate desire for a child or another child. In terms of climate change, no directional prediction was made. Available evidence from polling has suggested that climate change concerns should curtail reproduction,[1] whereas LHT and priming studies within the latter theoretical framework have suggested that the opposite pattern should occur.

MATERIALS AND METHODS

Participants

Using the online platform Prolific (Damer and Bradley, 2014),[2] a statistically representative sample of the UK population aged between 18 and 35 years was recruited. Using G*Power (Erdfelder et al., 1996), the sample size was determined with an anticipated "small effect" with 10 predictors (power = 0.95). Three hundred and twenty-five participants completed the online survey, but 26 declined to answer the COVID-19 experience questions and were removed from the study. Of the remaining 297 participants, 245 identified as White, 27 as Asian, 9 as Black, 9 as of mixed heritage, and 7 as "other." One hundred and fifty-seven participants were female. Participants were paid £3 for completing the survey. Data collection took place at the beginning of August 2020, around 4 or 5 months after the first UK national lockdown was declared in response to the COVID-19 pandemic.

Outcome Variables

The study measured three outcome variables relating to reproductive decision-making. Participants were asked to report their ideal number of children and what would be the ideal age at which to have their first child. For the third outcome variable, participants were asked whether the COVID-19 pandemic had affected their desire to have a child or another child on a scale of −3 (*much less desire*) to +3 (*much more desire*), which was coded 1–7 for analysis purposes and labeled "change in desire." Participants who did not want children were able to indicate this.

Predictor Variables

The extrinsic threat from COVID-19 was operationalized as the participant's reported experience with the illness. As per the pre-registration, there were two variables of interest. The first was whether participants believed they had caught COVID-19 (regardless of whether they had received a confirmed positive test result) and the degree of their symptoms: no or "don't believe so," mild symptoms, moderate symptoms, severe symptoms without hospital admission, or required hospitalization. A list of symptoms for each degree of severity was provided. Participants were then asked to indicate how many people close to them had experienced a (suspected) COVID-19 infection, including how many people had died or been hospitalized.

Existential threat was measured by views on climate change. Three predictor variables were collected. To measure "worry" about climate change, participants were asked Question 4 from the latest RESiL RISK survey of climate change attitudes (Steentjes et al., 2020): "How worried, if at all, are you about climate change?" Their answers were assessed using a scale from 1 (*not worried at all*) to 5 (*extremely worried*).

To measure "expectations" of climate change, participants responded to Question 17 of the same survey. This question was comprised of 16 items that asked participants to indicate on a scale of 1 (*very unlikely*) to 5 (*very likely*) how likely various outcomes of climate change were to occur in the United Kingdom (e.g., "Cities and large towns, which trap heat, becoming unbearably hot due to heatwaves"; $\alpha = 0.91$).

Participants were also assessed on their level of climate denialism using the dominance and climate change denial scale (Häkkinen and Akrami, 2014). While listed in the pre-registration, this questionnaire was excluded from the analysis because of low reliability ($\alpha = 0.55$).

[1]Schneider-Mayerson and Leong (2020) was published after the current study's registration and data collection had concluded.

[2]Demographic percentages were computed using Home Office statistics (ONS, 2018) with individual inclusion based on each participant's Prolific profile.

Covariates

To discern whether COVID-19 experience and climate change beliefs impact reproductive decision-making, several covariate variables were collected to act as controls in the General Linear Model. Participants were asked how many people they felt close to had died in the past 5 years prior to January 2020. Participants were also asked to indicate their perceived SES using the MacArthur Scale of Subjective Social Status (Singh-Manoux et al., 2003). This measure asks participants to imagine society as a ladder where those at the top have the best jobs, the most money, and the most opportunities and those at the bottom have the least (1 = *the very bottom* to 10 = *the very top*). Participants indicated their place on the ladder based on their current situation and their childhood situation. Participant age was also recorded.

Procedure

To ensure the COVID-19 and climate change questions did not influence participant responses to the critical reproductive decision-making questions, the survey was given in a specific order and all participants experienced the same order (although the arrangement of individual items was randomized). To further prevent the true nature of the study from being discerned, distractor items and questionnaires were also included.

Participants were first asked the three reproductive decision-making questions (see section "Predictor Variables"). To prevent the true nature of the study from being discerned, participants were also asked similar questions regarding home ownership, business ownership, large purchases (over £500), and retirement plans. Participants then completed the mini IPIP (Donnellan et al., 2006), which was the first of two distractor questionnaires,[3] followed by the "worry" and "expectation" climate change measures. Participants then completed the second distractor questionnaire, The Dirty Dozen (a short measure of the Dark Triad; Jonason and Webster, 2010), followed by the climate change denial scale. Participants then indicated how many of their close associates had died in the 5 years prior to January 2020, and then, they answered the COVID-19 questions. Finally, participants indicated their current SES and childhood SES.

Statistical Analysis

A GLM was used to investigate whether the COVID-19 experience and climate change belief variables predicted reproductive decision-making; the alpha threshold was set at $p < 0.017$ because there were three separate outcome variables. For all pre-registered analyses, age, sex, and both childhood and current SES were entered into the model as controls. While not predicted in the pre-registration, exploratory analyses were carried out to investigate whether any effects of extrinsic and existential risk on reproductive decision-making were moderated by childhood SES. Moderation analyses were conducted using PROCESS (Hayes, 2012). All analyses were conducted in SPSS 26.

[3]The mini IPIP (Donnellan et al., 2006) and The Dirty Dozen (Jonason and Webster, 2010) were included to avoid participants recognizing that the study was concerned specifically with beliefs about climate change.

Ethics

This study was conducted with the full ethical approval of the School of Psychology's (University of Chester) Research Ethics Committee. Participants gave written informed consent before taking part in the study; they were fully debriefed once their participation was complete and given the option to withdraw their data without penalty should they desire.

RESULTS

Sixty-seven participants already had children and 230 did not; no *a priori* assumption was made that the former would affect either "change in desire" or "ideal number of children," so they were included in those analyses. However, they were removed from the "ideal age" question since logically, COVID-19 could not have affected their decision. Of those who did not already have children, 36 participants indicated that they did not want children. Since no *a priori* assumption was made regarding those who wanted to remain childless (their decision could have been related to COVID-19, climate change, or some unrelated factor), they were included in the change in desire and ideal number of children analyses. However, they were excluded from the question regarding ideal age. Thus, all 297 participants were entered into the analyses of ideal number of children and change in desire for a child, and 196 participants were entered into the analysis of ideal age.[4]

The nature of the data required some departure from the pre-registered variables. Two hundred and nineteen participants reported not becoming sick from COVID-19, 49 believed they had experienced mild sickness, 24 believed they had experienced moderate sickness, three believed they had experienced severe symptoms, and two preferred not to say. As a result, the variable "own sickness" was converted into a dichotomous variable indicating whether the participant had become sick ($N = 78$) or not. Equally, only 49 participants indicated they knew at least one person who had either required hospital treatment or had died due to COVID-19. This variable was also converted into a dichotomous variable, labeled "other sickness." No other changes were made. Descriptive statistics for the continuous variables can be found in **Table 1**.

Ideal Number of Children

Evidence showed that experience with COVID-19 was associated with ideal number of children. As shown in the summary of the full model containing all predictors (**Table 2**), with all predictors entered, other sickness significantly predicted ideal number of children, with those who knew someone who had been hospitalized or died from COVID-19 reporting a greater number of children as ideal (Adj. $R^2 = 0.06$, $F_{9,287} = 2.19$, $p = 0.02$). However, following the recommendations of Achen (2005; see also Corpuz et al., 2020), the effect of each predictor was investigated separately along with the control variables. The only significant predictor of ideal number

[4]Two individuals who had children indicated they did not want children.

TABLE 1 | Descriptive statistics.

	Age	Ideal age[1]	Ideal number of children	Change in desire	Climate worry	Climate expectation	Bereavements	Current SES	Childhood SES
M	26.7	29.79	2.10	4.16	3.28	3.82	1.41	5.13	5.18
SD	5.16	3.38	1.17	1.32	1.02	0.65	1.52	1.69	1.89
Min.	18	22	0	1	1	1	0	1	1
Max.	35	40	7	7	5	5	8	9	10

[1]*Excluding participants who already had children or who do not wish to have children (N = 196).*

TABLE 2 | Summary of coefficients for full models.

	Ideal number of children			Change in desire for children		
	***b* (se)**	**BCa 95% CI**	***p***	***b* (se)**	**BCa 95% CI**	***p***
Constant	*3.15 (0.54)*	*2.08/4.20*	*<0.001*	*3.23 (0.78)*	*1.70/3.99*	*<0.001*
Own sickness[1]	0.12 (0.14)	−0.14/0.38	0.43	0.03 (0.19)	−0.38/0.40	0.86
Extreme exposure[2]	**0.39 (0.17)**	**0.07/0.72**	**0.02**	0.12 (0.25)	−0.39/0.57	0.60
Climate worry	0.03 (0.07)	−0.10/0.17	0.64	−0.16 (0.11)	−0.35/0.06	0.14
Climate expectation	−0.10 (0.11)	−0.32/0.13	0.37	**0.37 (0.17)**	**0.05/0.67**	**0.029**

Bereavement, age, sex, childhood SES, and current SES were held constant in all analyses. Bias-corrected 95% CI bootstrapped (5,000 sample). Reference category =[1]*Had not contracted COVID;* [2]*Did not know anyone who had been hospitalized with or died of COVID-19. Bold indicates p < 0.05.*

of children was whether participants knew someone who had become seriously ill with COVID-19 [other sickness: $R^2_{\text{Adjusted}} = 0.06$, $F_{6,290} = 3.07$, $p = 0.006$; $b = 0.42$, $SE = 0.18$, BCa 95% CI (0.07/0.76), $p = 0.016$]. The latter model can be considered the most parsimonious and falls under our conservative threshold for significance, although this approach was not specified in the pre-registration. There was no evidence that climate change belief was associated with ideal number of children.

Change in Desire for a (Another) Child

There was no clear evidence that any of the predictor variables were associated with a change in the desire for a child. As shown in **Table 2**, in the full model, the "climate expectation" variable did show a significant relationship with change in desire, with a greater expectation of negative consequences from climate change predicting an increase in the recent desire to have children. However, there was no overall significant model fit ($R^2_{\text{Adjusted}} = 0.01$, $F_{9,287} = 1.19$, $p = 0.30$). Equally, when each predictor was entered individually into a model with the control variables, none were significant. Thus, no predicted variable can be claimed to have had a relationship to change in desire.

Ideal Age for First Child

No measures of COVID-19 experience or climate change belief were associated with the ideal age to have children. However, there was a strong positive correlation between participant age (minus the exclusions, $M = 25$, $SD = 5$, Min. = 18, Max. = 35) and ideal age to have a first child [$r = 0.56$, $N = 196$, $p < 0.001$, BCa 95% CI (0.45/0.66)]. In the model and moderation analyses, participant age was the sole predictor of ideal age ($p < 0.001$).

Exploratory Analysis: Moderating Effects of Childhood SES

The primary aim of the current study was to investigate extrinsic and existential risk based on whether cues of risk (i.e., severe COVID-19 infection in oneself or one's associates) and beliefs about climate change were associated with reproductive decision-making. Nevertheless, given the established association between risk and early life stress, exploratory analyses were also conducted to investigate whether such effects were present in the data. As the study cannot be considered appropriately powered to detect such interactions (Achen, 2005; Giner-Sorolla, 2018), the results should be interpreted with caution.

Table 3 shows GLMs with each individual variable and controls and an interaction between childhood SES and the variable. As shown in **Table 3**, the relationship between other sickness and ideal number of children was not moderated by childhood SES, with other sickness remaining a significant predictor of ideal number of children with the interaction included in the model. Childhood SES did not moderate the relationship between own sickness and ideal number of children (**Table 3**).

As shown in **Table 3** and **Figure 1**, childhood SES moderated the relationship between climate worry and ideal number of children. However, a simple slopes analysis showed there was no relationship between climate worry and ideal number of children at high, average, or low levels of childhood SES ($p > 0.05$). Using the Johnson–Neyman (J–N) technique to further probe for sensitivity (Hayes and Matthes, 2009), the J–N point for $p < 0.05$ of childhood SES occurred at −4.32 and +3.82 of the mean. The region of significance contained 2% of the sample.

TABLE 3 | Moderating effect of childhood SES on ideal number of children.

Models		R^2	*F* (df)	*p*	Boot *b* (se)	Boot 95% CI
1.	Own sickness					
	Constant	**0.06**	**2.49 (7,289)**	**0.017**	*2.83 (0.37)*	*2.10/3.54*
	Own sickness[1]				0.18 (0.14)	−0.09/0.46
	Childhood SES				−0.01 (0.04)	−0.07/0.09
	C.SES*own sickness				−0.15 (0.08)	−0.31/0.007
2.	Other sickness					
	Constant	**0.06**	**2.69 (7,289)**	**0.01**	*2.79 (0.37)*	*2.05/3.51*
	Other sickness[2]				**0.40 (0.17)**	**0.06/0.74**
	Childhood SES				−0.01 (0.04)	−0.09/0.07
	C.SES*extreme exposure				−0.05 (0.10)	−0.26/0.13
3.	Climate worry					
	Constant	**0.05**	**2.36 (7,289)**	**0.02**	*2.87 (0.38)*	*2.16/3.58*
	Climate worry				0.01 (0.06)	−0.10/0.15
	Childhood SES				−0.02 (0.04)	−0.10/0.05
	C.SES*climate worry				**0.07 (0.03)**	**0.00/0.14**
4.	Climate expectation					
	Constant	0.05	2.02 (7,289)	0.052	*2.89 (0.40)*	*2.10/3.68*
	Climate expectation				−0.06 (0.10)	−0.24/0.13
	Childhood SES				−0.03 (0.04)	−0.10/0.05
	C.SES*climate expectation				0.07 (0.05)	−0.30/0.16

Bereavement, age, sex, and current SES were held constant in each analysis. All non-dichotomous variables were mean centered and bootstrapped (5,000 sample). Reference category =[1]Had not contracted COVID-19; [2]Did not know anyone who had been hospitalized with or died of COVID-19. Bold indicates p < 0.05.

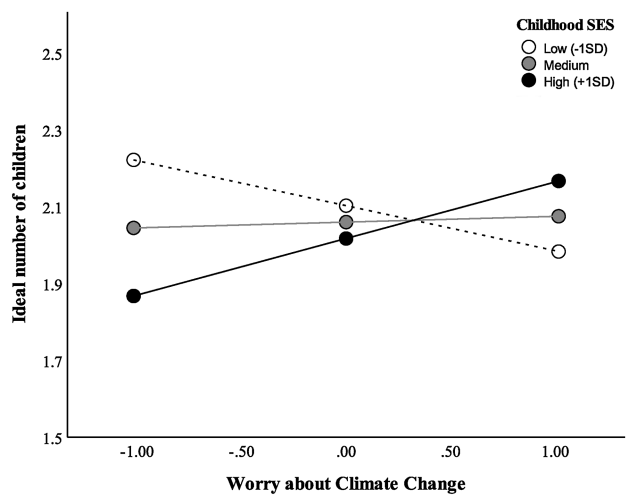

FIGURE 1 | Relationship between ideal number of children and worry about climate change, moderated by childhood SES.

No moderating effects were found for the reproductive decision-making variables ideal age or change in desire.

DISCUSSION

The current study investigated the impact of extrinsic and existential mortality risk on reproductive decision-making in a WEIRD population. In line with LHT, it was predicted that COVID-19 experience (extrinsic risk) would be associated with responses indicative of a faster life history, with greater experience being associated with a greater ideal number of children, a lower ideal age at which to have children, and a recent increase in the desire to have a child or another child. It was also predicted that beliefs about climate change (existential risk) would be associated with reproductive decision-making, although no directional predictions were offered due to conflicting evidence (Schneider-Mayerson and Leong, 2020). Some of these predictions were supported.

Extrinsic Risk and Reproductive Decision-Making (COVID-19 Experience)

The results suggested that being close to someone who was seriously ill or died from COVID-19 was associated with a greater ideal number of children. This association supports both the prediction of the study and previous research on the role of life history in reproductive decision-making. Research has shown that local cues of mortality risk affect reproductive decision-making (Quinlan, 2010; Pepper and Nettle, 2013; McAllister et al., 2016), and knowing individuals who were seriously ill or died from COVID-19 serves as a cue of an elevated risk of mortality in the environment. As such, the result suggests that even a brief change in extrinsic risk can potentially result in a faster life history. For obvious reasons, the experimental literature on the effect of mortality risk has relied on primed cues of mortality (Wisman and Goldenberg, 2005; Mathews and Sear, 2008; Griskevicius et al., 2011), thus limiting the ecological validity of the findings. The current study supports the conclusions of these studies by demonstrating the relationship between an actual sudden change in extrinsic mortality risk (i.e., the COVID-19 pandemic) and reproductive decision-making. More broadly, the results also provide further empirical support for adult changes in

life history due to changes in extrinsic risk (Pepper and Nettle, 2013).

There has been some debate as to what exactly acts as a cue to mortality risk (Pepper and Nettle, 2014; Chipman and Morrison, 2015; Wu et al., 2020). Research thus far has suggested that participants understand that COVID-19 poses a real risk to health (see Sutton and Douglas, 2020). As such, it is interesting that COVID-19 experience predicted reproductive decision-making—or rather, that the dramatic change in everyday life and the daily reported death toll did not raise the floor of responses sufficiently for no effect to be detected. Conversely, at the time of data collection in early August 2020, the United Kingdom was at the bottom of the first wave of the pandemic, and the focus was on returning to "normal" life (e.g., there was a scheme offering discounts on restaurant meals; see "Eat Out to Help Out," HM Treasury, 2020), and news of vaccine successes may have given the impression that the crisis would be over soon (University of Oxford, 2020). Both factors could have lowered the ceiling on the perceived current and future risk from COVID-19. The results therefore highlight that despite a media environment saturated with COVID-19 information, a change in life history was associated with a close experience of mortality cues.

While the study used COVID-19 infection to operationalize extrinsic risk, susceptibility to disease is also an intrinsic risk. Intrinsic risk—meaning risks dependent on internal factors or personal behavior—has also been shown to impact life-history strategy. For example, MHC homozygosity (Murray et al., 2017) and a history of vulnerability to illness (Hill et al., 2015) have been linked with a faster life history, and some research has associated immunocompetence with childhood SES (Rubika et al., 2020). Equally, Corpuz et al. (2020) found that a fast life history was associated with less engagement with and endorsement of health advice. As such, we may have expected childhood SES—a factor predictive of a faster life history (e.g., Griskevicius et al., 2011)—to have moderated the relationship between the COVID-19 variables and reproductive decision-making. Such a relationship was not found, but this may have been due to the lack of statistical power to detect interaction effects. A higher-powered examination of how COVID-19 infection might differentially affect those with a faster lift history is certainly warranted.

No relationship was found between COVID-19 experience and the other outcome variables regarding the ideal age at which to have the first child or whether the desire for a child had changed since the beginning of the pandemic. For the latter, it does appear contradictory that COVID-19 exposure would predict an increase in the ideal number of children but not in the reported change in desire. The reason may be due to the construction of the question. Most studies have asked participants about their general future desire (Wisman and Goldenberg, 2005; Griskevicius et al., 2011), whereas the question created for the current study asked participants to think very specifically about their current circumstances. Thus, the results might represent a difference between generality and specificity when eliciting responses: Asking participants to "think about the last 6 months" required a more specific examination of their immediate situation compared to the question "what is your ideal number of children?" Importantly, this supposition is supported by the data from previous pandemics where there is a brief reduction in births before a "boom" (Ullah et al., 2020). Thus, asking participants to consider their immediate circumstances produced different responses compared to asking a general question about family planning.

There is a more straightforward explanation for the lack of any associations between COVID-19 experience and ideal age of first birth—COVID-19 is a sudden and very recent event. Past studies examining mortality cues and reproductive decision-making have operated over a larger window in terms of the type of environmental risk studied, and they have typically included younger age groups (Pepper and Nettle, 2013; Häkkinen and Akrami, 2014; Virgo and Sear, 2016). Given the plethora of proximate factors affecting reproductive scheduling in post-demographic transition societies (e.g., Burnside et al., 2012; Sear et al., 2016), it may be that the demographic window of the current sample was too narrow for any effect of COVID-19 on reproductive scheduling to be apparent. Indeed, the mean age at first childbirth in the United Kingdom is 29 years (ONS, 2019), which is not far from the mean age of the participants, and the analyses showed that ideal age was solely predicted by actual age.

Still, the demographics of the study do provide room for COVID-19 experience to influence life history. It was predicted that an increase in extrinsic mortality risk would be associated with all aspects of reproductive decision-making, and the prediction regarding ideal age at first birth was not supported. That only one of the three metrics of reproductive decision-making showed the predicted relationship with COVID-19 experience should be taken into consideration when drawing any conclusions about the impact of COVID-19 on life-history strategies. Nevertheless, with other factors that affect life history controlled for, knowing others who had become seriously ill with COVID-19 was related to the number of children the participants desired, even if it was not related to the age at which they planned to start.

Existential Risk and Reproductive Decision-Making (Climate Change)

There was no indication that climate change beliefs were associated with reproductive decision-making overall, which would be expected based on the results from previous studies that have primed precarious, although non-specific, futures (McAllister et al., 2016). One of the key tenets of LHT is that the early childhood environment and the immediate environment provide cues to the future to which organisms are sensitive (Del Giudice et al., 2015; Pepper and Nettle, 2017; Nettle and Frankenhuis, 2020). However, recognizing the real possibility of global human extinction is a new phenomenon. The evolutionary novelty of existential risk potentially means that human existence does not influence life-history strategy as we might have logically surmised (Li et al., 2018; Schubert et al., 2019; Young et al., 2020). Indeed, the exploratory moderation analyses suggested that the moderating effects of childhood SES on the relationship between the ideal number

of children and worry about climate change ran counter to what would be expected according to LHT.

The reproductive decision-making responses to the very salient and (at the time of writing) ongoing COVID-19 pandemic were predicted by direct experience. However, worrying about future outcomes of climate change is very different from worrying about a measure of local violent crime or being asked to imagine one's own death, for example. Thus, due to their novelty, concerns about existential risks might simply not act as reliable cues of future or present instability as imagined by LHT (Young et al., 2020). Indeed, evidence from a US sample suggested that the experience of extreme weather events was not reflected in concerns about climate change (Brulle et al., 2012). Instead, any response to more abstract existential thoughts (potentially "slow" thoughts; Kahneman, 2011) about the future might be better set in the context of resource allocation in post-demographic transition societies (e.g., Burnside et al., 2012; Sear et al., 2016). Interestingly, while it has been suggested that existential risk is an evolutionary novelty, the moderation by childhood SES observed in this study (albeit for only one of the outcome variables) is potentially similar to historical patterns of reproductive decision-making in resource-limited environments (Volk, 2021). The study is not able to address this debate further, but it is a question certainly worth exploring.

The lack of any concrete results regarding climate change and reproductive decision-making does contradict the little evidence that exists on this topic (Schneider-Mayerson and Leong, 2020). This is likely due to methodological differences, as Schneider-Mayerson and Leong (2020) recruited participants through a largely US-based activist network and emphasized policy issues (e.g., the carbon footprint of a child). Unsurprisingly, that sample reported higher climate change concerns than the sample in the current study and compared to the UK population in general (see Steentjes et al., 2020). Thus, if there is one conclusion that can be drawn from the climate change data, it should be that the reports of climate change concerns reducing the desire to have children are perhaps premature.

Future Directions

While the study aimed to investigate the relationship between extrinsic and existential risk and reproductive decision-making, the measures of each were very different. Extrinsic risk was operationalized as COVID-19 experience, whereas existential risk was measured through attitudinal questionnaires. As such, the current study did not ask about any experiences with climate change (e.g., destruction of property due to flooding). However, once this occurs, climate change arguably becomes an extrinsic mortality risk. Semantic arguments notwithstanding, it should be possible to investigate existential risks without engaging in such a debate. Future cross-sectional research might wish to investigate whether living in environments associated with existential risk cues (e.g., along coastlines or near nuclear weapons facilities) is associated with faster life histories. Finally, while climate change might lead to both a harsh and unpredictable future, the childhood SES measure used in the study can be indicative of a harsh early environment but not necessarily an unstable one (see Young et al., 2020). Measures of early life instability may yield different patterns of interaction between that variable and measures of local mortality (e.g., COVID-19) and climate change beliefs.

Equally, with its cross-sectional design, the current study cannot demonstrate causation. Building on the methodologies of prior work (e.g., Griskevicius et al., 2011), experimental research might investigate whether priming participants with existential risks produces results that are contrary to or in accordance with LHT, such as priming for existential risk in general, for specific possible consequences (e.g., personal property damage or contact with displaced populations, see Vardy and Atkinson, 2019), or to make the risk to future offspring especially salient.

Furthermore, as the results for climate change belief did not correspond to either LHT or the limited sociological data available, it is possible that two forces are acting against one other regarding reproductive decision-making: Existential risk cues might be unconsciously inducing a faster life history, while conscious thought regarding children's future experiences might be reducing the desire to have them. The current study was not designed to investigate this, but future work examining interactions between existential beliefs and morality cues would certainly help shed further light on the place of existential risk within the LHT framework.

Finally, the current study was conducted using a representative sample of a WEIRD society (i.e., the United Kingdom). Doing so allowed for an investigation of life-history responses to a sudden national increase in mortality risk in a population that had not experienced such a change in generations. Still, a relationship has been found between broader ecological factors, such as climate and pathogen load, and life histories (Luoto et al., 2019b), and any future cross-cultural investigations of the legacy of the pandemic should take such factors into account. It is also important to note that numerous WEIRD and non-WEIRD populations are already experiencing the negative effects of climate change (Dannenberg et al., 2019). Additional research within these populations would also help further address the questions raised by the current study.

Conclusion

The study investigated the impact of extrinsic mortality risk (experience of the COVID-19 pandemic) and existential risk (beliefs about climate change) on reproductive decision-making in a WEIRD society. In line with LHT, COVID-19 experience was associated with a greater ideal number of children. Beyond providing further empirical support for the utility of LHT in understanding human behavior, the current study provides important practical considerations for any policy response to the COVID-19 pandemic. Over a year into the pandemic, the media (Meredith, 2021) and policymakers (Public Health England, 2021) have focused on its consequences for mental health, but by demonstrating that COVID-19 exposure is associated with reproductive decision-making, the results of this study suggest that COVID-19 experience will have broader implications for a wide range of behaviors associated with life-history strategies. Further research on this topic will be vital in understanding the long-term consequences of the pandemic.

The study did not find any consistent evidence of a relationship between existential risk and reproductive decision-making. Given the urgency of climate change and other existential risks (Bostrom, 2002), additional research is warranted to examine further how evolved responses interact with this form of risk and what form those responses take. This is especially vital to understand since faster life-history strategies will arguably be counter-productive to find any global solutions as the everyday impact of climate change becomes increasingly apparent (i.e., as it becomes an extrinsic risk).

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 at Open Science Framework. Project title: Extrinsic and existential mortality risk in reproductive decision-making. Available at: https://osf.io/ytx9d/.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the School of Psychology's (University of Chester) Research Ethic Committee. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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Why Do People (Not) Engage in Social Distancing? Proximate and Ultimate Analyses of Norm-Following During the COVID-19 Pandemic

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COVID-19 has had a profound negative effect on many aspects of human life. While pharmacological solutions are being developed and implemented, the onus of mitigating the impact of the virus falls, in part, on individual citizens and their adherence to public health guidelines. However, promoting adherence to these guidelines has proven challenging. There is a pressing need to understand the factors that influence people's adherence to these guidelines in order to improve public compliance. To this end, the current study investigated whether people's perceptions of others' adherence predict their own adherence. We also investigated whether any influence of perceived social norms was mediated by perceptions of the moral wrongness of non-adherence, anticipated shame for non-adherence, or perceptions of disease severity. One hundred fifty-two Australians participated in our study between June 6, 2020 and August 21, 2020. Findings from this preliminary investigation suggest that (1) people match their behavior to perceived social norms, and (2) this is driven, at least in part, by people using others' behavior as a cue to the severity of disease threat. Such findings provide insight into the proximate and ultimate bases of norm-following behavior, and shed preliminary light on public health-related behavior in the context of a pandemic. Although further research is needed, the results of this study—which suggest that people use others' behavior as a cue to how serious the pandemic is and as a guide for their own behavior—could have important implications for public health organizations, social movements, and political leaders and the role they play in the fight against epidemics and pandemics.

Keywords: perceived norms, pathogen avoidance, behavioral immune system, conformity, proximate-ultimate, pandemic, COVID-19, public health

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INTRODUCTION

The World Health Organization (WHO) declared COVID-19 a pandemic on March 11, 2020 (World Health Organization [WHO], 2020a). Since then, the pandemic has had a profound negative impact on many aspects of human life. At the time of writing, the human toll has surpassed three million lives (World Health Organization [WHO], 2020b). This pandemic resulted in unprecedented economic shutdowns, leaving many

countries facing fiscal uncertainty (Australian Bureau of Statistics, 2020). Some countries were initially successful in their efforts to limit the spread of the disease, but many have subsequently faced second and even third waves, with uncertainty and concern remaining about further waves (see Xu and Li, 2020).

Given the societal impact of COVID-19 and the role individual citizens play in curtailing infectious diseases, it is essential to understand the psychological processes involved in people's adherence to pandemic mitigation guidelines (Bavel et al., 2020). Such an understanding could help scaffold to a more in-depth, comprehensive program of research and inform public policy on prevention strategies. Further, insights into these psychological processes could improve COVID-19 messaging in public health initiatives.

Methods and Challenges in Managing the Spread of a Pandemic

Current methods for controlling the spread of a pandemic involve developing and implementing pharmacological treatments and vaccines, increasing hygiene practices, risk communication (Taylor, 2019), closures of public places, voluntary/mandated quarantines (Lu et al., 2021), contact tracing, rapid testing, and herd immunity through exposure (a controversial approach currently only tested in Sweden; Anderson et al., 2020; Habib, 2020). While there are a number of promising vaccines currently in production, even the most optimistic projections tell us that we will not be able to achieve population immunity on a global scale (60–80% of the population) by the end of 2021 (Wang et al., 2020). While vaccine programs are rolled out, top-down policies will be important for limiting the spread of COVID-19 (see Wilson, 2020; Lu et al., 2021; Luoto and Varella, 2021), but the efficacy of these policies may rest largely on the choices of individual citizens to adhere (or not) to these guidelines. To facilitate this, the WHO put forward a global action plan aimed at limiting the spread of COVID-19 through individual behaviors (World Health Organization [WHO], 2020c). This plan emphasizes the uptake of non-pharmacological interventions (NPIs; e.g., frequent handwashing, social distancing, and self-isolating when unwell) at the individual level (World Health Organization [WHO], 2020c). However, it is not clear that these guidelines were informed by an understanding of the psychological processes that influence individual-level decisions to adhere (or not) to NPIs. Public uptake of NPIs has been highly variable. Some populations have reported adherence rates as high as 90% (see Lennon et al., 2020), whereas others have reported rates of adherence as low as 67%—indicating that 1 out every 3 individuals is not adhering to guidelines (see Block et al., 2020).

In previous pandemics, the uptake of these NPIs has been an uphill battle for the public health sector (Gilles et al., 2011; Mitchell et al., 2011; Steelfisher et al., 2012). In general, people routinely fail to follow handwashing recommendations (Pfattheicher et al., 2018). During the 2009 swine flu pandemic, people who believed that they were in the "low risk" category for infection were less likely to engage in handwashing (Gilles et al., 2011). Another study conducted at the same time found that less than 10% of people with acute respiratory infections stayed home when symptomatic, and as many as 45% of people reported attending social events because they did not believe they were contagious (Mitchell et al., 2011). Even during highly lethal outbreaks, such as the African Ebola virus epidemic, some families sheltered sick relatives at home instead of sending them to quarantine facilities (Shultz et al., 2015). This trend of mixed adherence is reflected in the COVID-19 pandemic. For example, media in the United States, Germany, New Zealand, Belgium, England, and France have all reported an increase in social gatherings following lockdowns (Ölcer et al., 2020). Even the WHO has acknowledged that advising sick people to remain home during a pandemic may be impractical and frequently ineffective (World Health Organization Writing Group, 2012).

These issues highlight the need to gain a better understanding of the predictors of NPI adherence and non-adherence. In the context of a highly transmissible and dangerous virus like that responsible for COVID-19 (Petersen et al., 2020), one individual's non-adherence to NPIs could have widespread negative effects for others. Public health messaging has focused on this fact as a key motivator in NPI adherence, a sentiment reflected in the prominent WHO campaign message "Protect yourself and others" (World Health Organization [WHO], 2020d). However, the effectiveness of this approach depends on people's desire to minimize the collective harm of COVID-19. Such a strategy may be somewhat naïve in the face of evidence suggesting that collective harm minimization tends to be a weak motivator for behavior change (Markowitz and Shariff, 2012; Yong and Choy, 2021). Consequently, there is a scientific and public health need for research that identifies predictors of adherence to NPIs during the COVID-19 pandemic. Work has already begun on this front (e.g., see Corpuz et al., 2020; Dinić and Bodroža, 2021; Varella et al., 2021; Yong and Choy, 2021), but a collective effort by researchers working in parallel is needed to rapidly map the individual difference, situational, and other psychological and environmental variables that explain why some people adhere to NPIs, whereas others do not.

One particularly important factor may be perceived social norms (Bavel et al., 2020). This factor may help explain, at a proximate level, why adherence is so mixed: perceived norms can vary substantially across individuals (see Miller and Prentice, 1996). We are unaware of any research, to date, that has investigated perceived norms as a potential explanation for NPI adherence (or non-adherence) during the COVID-19 pandemic. To address this gap in the literature, the present study investigated (1) the relationship between perceived norms and people's adherence to NPIs and (2) several plausible psychological processes that might be responsible for a link between people's perceptions of others' adherence and their own decisions to adhere (or not).

To gain a more in-depth understanding of norm-following behavior, our investigation considers both the proximate and ultimate levels of analysis. Currently, social psychology literature tends to explain norm-following behavior (e.g., conformity) only in proximate terms (e.g., features of the immediate social context) but offers little in the way of ultimate explanation (i.e., why people have cognitive systems for processing and responding to information from the social environment in that way in the

first place) (for an in-depth discussion of proximate/ultimate explanations, see Scott-Phillips et al., 2011; Lewis et al., 2017; Al-Shawaf et al., 2019).

Hypothesis 1: People Mimic Perceived Normative Behavior

It is well-established that social norms influence people's behavior (Miller and Prentice, 1996), including in the context of disease prevention. Evidence suggests that people's frequency of engaging in specific disease-prevention behaviors is associated with their perceptions of their peers' frequency of engaging in those behaviors (Dickie et al., 2018). Research also suggests that social networks can amplify the spread of beneficial as well as harmful health behaviors during epidemics (Christakis and Fowler, 2013). Together, these pieces of evidence suggest that people's perceptions of others' adherence may influence their own adherence to NPIs during the COVID-19 pandemic. This is the overarching hypothesis of the current study: people mimic behavior that they perceive as normative (Hypothesis 1). This leads to the prediction that people's current adherence to NPIs should be positively associated with their perceptions of others' adherence (Prediction 1.0).

However, if this is correct, *why* does it happen? That is, what are the ultimate origins of such norm-following behavior? Here, we present several alternative, but not necessarily mutually exclusive, mechanisms that could be responsible for a link between people's perceptions of norms and their own behavior.

Hypothesis 1.1: The Threat of Social Exclusion Influences People's Adherence to NPIs

A prominent finding in social psychology is that violation of social norms invites direct or indirect punishment (Perreau De Pinninck et al., 2007; Rudert et al., 2019). One particularly effective form of punishment is ostracism of those who deviate from group norms (Rudert et al., 2019). Social exclusion is a physiologically harmful and psychologically distressing experience for the target (Williams, 2007; Nezlek et al., 2012). In ancestral small-scale hunter-gatherer contexts, ostracism from the group would often have been deadly (Spoor and Williams, 2007; Williams, 2007). Consequently, selection may have favored a "detection system" capable of identifying the threat of ostracism and preventing it from occurring (see Spoor and Williams, 2007; Wesselmann et al., 2012). Consistent with this proposal, people take action to avoid social exclusion whenever possible (Wesselmann et al., 2012).

A consideration of the social group living conditions thought to characterize much of our species' evolution can also offer insight into why people are ostracized for norm violations in the first place. In ancestral environments, norms of cooperation were essential to group survival (Wesselmann et al., 2012). Many deviations from these norms (e.g., free riding on the benefits of collective efforts) would have been detrimental to other group members (Wesselmann et al., 2012). The proposed ultimate function of ostracism—to punish norm-violators who are inflicting fitness costs on other group members, including oneself—may help explain why neutral observers tend to regard ostracism of norm violators as legitimate when said ostracism serves the benefit of the group (Williams et al., 1998).

In the context of COVID-19, NPI adherence can be conceptualized as a public goods game (see Yong and Choy, 2021). All benefit from others' adherence, but those individuals who themselves do not adhere to NPIs reap these benefits without incurring the costs of adherence: they are free riders. High levels of adherence to NPIs are crucial to their efficacy; a single individual who engages in such free-riding behavior by not following NPI guidelines can undermine the collective effort. If the psychological mechanisms responsible for ostracizing others marginalize those individuals who violate norms to the detriment of other group members, then those members of society who do not align their behavior with the coordinated actions of others may face the threat of ostracism.

In turn, the threat of being ostracized for disrupting group coordination is a key activator of the shame system (see Robertson et al., 2014). The human shame system operates like a sentinel, vigilantly scanning for cues that indicate the threat of social devaluation (Robertson et al., 2018) and triggering a suite of cognitive, affective, and behavioral responses to mitigate devaluation (see Sznycer, 2019 for a comprehensive description of shame as an internal, behavior-regulating emotion). In the context of the COVID-19 pandemic, if people perceive adherence to NPIs to be the group norm, and the threat of being ostracized for violating group norms activates the shame program, then we should expect people to anticipate experiencing shame for not following NPIs (see Robertson et al., 2014).

If this hypothesis (Hypothesis 1.1) is correct, there should be a positive association between (1) people's perception of others' adherence to NPIs and the shame they anticipate they would experience if they failed to adhere (Prediction 1.1.1), as well as between (2) people's anticipated shame and their reported adherence to NPIs (Prediction 1.1.2). This hypothesis also yields one more prediction: people's anticipated shame for non-adherence will partially mediate the relationship between their perceptions of others' adherence and their own adherence (Prediction 1.1.3).

However, the ostracism-avoidance hypothesis is not the only possible explanation for why individuals may match their behavior to what others are doing. A second possibility is that people may use others' behaviors as an indication of what is "right" or moral.

Hypothesis 1.2: People Regard Normative Behavior as a Cue to What Is Moral, and This Influences Their Adherence to NPIs

Evolutionary analyses of moral psychology suggest that certain facets of moral cognition serve to coordinate side-taking in disputes, and that these cognitive systems use other people's public behaviors to help determine which side they will take (see DeScioli and Kurzban, 2013). At an ultimate level of analysis, knowing which side others will take is key. Being on the wrong side—on this view, the minority side—of a dispute could have had

considerable negative fitness consequences (e.g., ostracism from the group, punishment, or death; DeScioli and Kurzban, 2013). By contrast, being on the side of the majority—that is, adhering to the group norm—would have helped immensely in avoiding these fitness costs (see Bocian and Wojciszke, 2014).

At an ultimate level of analysis, this suggests that certain facets of human moral cognition may have evolved to take, as input, other people's positions on an issue in order to regulate one's own behavior in a manner that safely avoids the costs associated with violating group norms. At a proximate level of analysis, this suggests that these moral cognitive systems will (a) take, as input, others' behavior and (2) produce, as output, perceptions of morality that track these perceived group norms and motivate behavior to align with these norms.

If this line of reasoning is correct, then (1) there should be an association between people's perceptions of others' adherence to NPIs and their perceptions of the moral wrongness of non-adherence (Prediction 1.2.1), (2) there should be an association between people's perceptions of the moral wrongness of non-adherence and their own adherence (Prediction 1.2.2), and (3) the predicted relationship between people's self-reported adherence and their perceptions of others' adherence will be at least partially mediated by perceptions of the moral wrongness of non-adherence (Prediction 1.2.3).

Hypothesis 1.3: People Use Others' Behavior to Gauge Disease Severity

Another possibility is that people observe others' rate of adherence to NPIs and use this information as a cue to the severity of disease threat. Such an explanation would be in line with social learning theory; one of the core principles of Vygotsky's (1978) work was the idea that others have information that we ourselves do not have, and contemporary social learning theory research highlights the importance of observation-based acquisition of knowledge (Csibra and Gergely, 2007). This perspective from social learning theory—which emphasizes the proximate level of explanation—is compatible with evolutionary reasoning focused on ultimate-level explanations. The parasite stress theory of sociality (Thornhill and Fincher, 2014) posits that humans possess a suite of social tactics to minimize the risk posed by pathogens in the local environment. This theory may shed light on why people would imitate others' behavior in the context of a pathogen threat. In the framework of this theory, people may use information about the behavior of other members of their group in order to gauge the severity of the disease threat (see Navarrete and Fessler, 2006).

Hypothesis 1.3 is thus that people use others' behavior as a cue to disease severity, and therefore as a guide for their own behavior. If this is correct, then (1) there should be an association between people's perception of others' adherence and their perception of the severity of COVID-19 (Prediction 1.3.1), (2) there should be a relationship between people's perceptions of the severity of COVID-19 and their own adherence (Prediction 1.3.2), and (3) the relationship between people's perception of others' adherence and their own adherence should be, at least, partially mediated by perceptions of the severity of COVID-19 (Prediction 1.3.3).

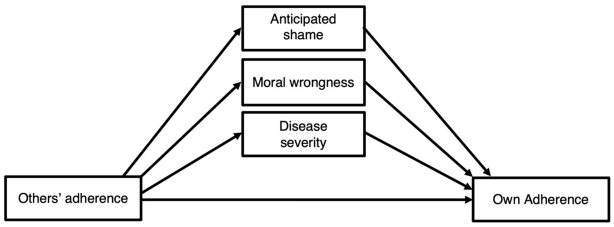

FIGURE 1 | Conceptual model illustrating possible pathways from perceived social norms to NPI adherence.

The Current Study

The current study sought to (1) determine whether people's perceptions of others' adherence predict their own adherence, and (2) identify the pathways that might mediate this relationship: through the threat of social exclusion, through perceptions that normative behavior is morally right, or through perceptions of disease severity (**Figure 1**).

MATERIALS AND METHODS

Ethics Statement

This study was approved by the Murdoch University Human Research Ethics Committee (Approval 2020/049).

Participants

One hundred seventy-three participants enrolled to participate in the study between June 6, 2020 and August 21, 2020. Participants ranged in age from 18 to 75 (M = 33.05, SD = 16.22), and represented all but one state and one territory in Australia (59% from Western Australia, 28% from Victoria, 6% from New South Wales, 4% from Queensland, and 1% from the Australian Capital Territory; three participants (2%) did not indicate their state of residence). Participants were recruited through the Murdoch University research participant portal, advertising on social media (Facebook), and snowball sampling. Participants who completed the survey through the Murdoch University research participant portal were granted partial course credit. Participants who were recruited through social media and snowball sampling were not provided any compensation.

Questionnaire and Procedure

As part of a longer survey investigating the psychological antecedents and consequences of the COVID-19 pandemic, participants completed the measures below via an online questionnaire on the Qualtrics XM platform. The survey was optimized for mobile phones as, given strict lockdowns, computer access may have been limited for participants from low socio-economic backgrounds and those who did not have access to a personal device at home (Raza et al., 2017).

The primary variables measured in the current study were participants' self-reported adherence to NPIs, perception of others' adherence to NPIs, perceptions of the seriousness of COVID-19, anticipated shame for non-adherence to NPIs, and perceptions of the moral wrongness of non-adherence. Participants were asked about four NPIs: handwashing, social distancing, quarantining following a positive COVID-19 test, and quarantining following a housemate's positive COVID-19 test. These four NPIs represent the recommendations put forward in the WHO's action plan (World Health Organization [WHO], 2020d); the WHO's revision to include mask wearing occurred after data collection began.

Others' Adherence

To measure perception of others' adherence, participants were asked to rate what percentage of the people in their country they thought were following NPIs. The exact wording used was *What percentage of people in your country do you think are now following the recommendations below*? For each of the four NPIs, participants answered on a percentage scale of 0–100% (of the population).

Own Adherence

To measure current adherence to NPIs, participants were asked to rate how strictly they were currently following the NPIs. The exact wording of this item was: *How strictly are you now following the recommendations below*? Participants provided answers on a 7-point Likert-type scale (1 = Never, 7 = Always). For these questions, participants were only asked about handwashing and social distancing, as only a small fraction of the population of interest (i.e., Australia) was advised to self-quarantine (e.g., when returning from international travel, experiencing flu-like symptoms, awaiting a result for a COVID test, or having had direct contact with someone with COVID-19).

Disease Severity

To measure participants' perceptions of the seriousness of COVID-19, they were asked: *How serious do you think COVID-19 is for public health now*? (1 = Not serious at all, 7 = Very serious).

Anticipated Shame

We modeled our measure of anticipated shame on Sznycer et al. (2018)'s cross-cultural study in which they presented participants with a series of scenarios and asked participants to "indicate how much shame you would feel if you were in these situations." The exact wording we used was: *How much shame do you think you would experience for doing this*? Participants responded on a 7-point Likert-type scale (1 = No shame at all, 7 = A great deal of shame).

Moral Wrongness

Following anticipated shame, participants were asked how morally wrong they perceived non-adherence to be. We based our measure of moral wrongness on DeScioli et al. (2011), who asked participants to rate the moral wrongness of specific behaviors on a 7-point scale ranging from 1 (not morally wrong at all) to 7 (very morally wrong). The exact wording we used was: *How morally wrong is this behavior*? (1 = Not morally wrong at all, 7 = Extremely morally wrong).

Recruitment Time Frame

Data collection for the present study occurred between June 6, 2020 and August 21, 2020.

Data Preparation and Analysis

Participants' data were excluded if they did not complete the full questionnaire (n = 12) or if they completed the survey in < 450 s (i.e., the time it would take to click through the survey without reading the questions) (n = 3). We also only included participants who indicated that they were currently living in Australia. This was because study measures were based on the NPIs being recommended at the time of data collection by the Australian government; these NPIs may not have included NPIs being mandated in others countries (e.g., mask wearing) as well as because of between-country differences in the distance specified for social distancing (e.g., 1.5 m vs. 6 ft). For these and other reasons, the data from six participants who indicated that they were living in a country other than Australia were not included in study analyses. These data preparation procedures yielded a final sample size of 152 participants. Missing data was excluded on a case-by-case basis because the different scales were measuring distinct constructs (Kang, 2013).

For data analysis, we focused exclusively on the NPI of social distancing. This was for several reasons. First, the questionnaire did not collect data on participants' self-reported adherence to self-quarantine. Second, although handwashing was one of the NPIs, it was a behavior that individuals would have engaged in prior to the pandemic. Without knowledge of participants' pre-pandemic frequency of handwashing, it would have been difficult to determine to what extent their current handwashing frequency reflected NPI adherence rather than their behavioral and personality patterns unrelated to the pandemic. Conversely, social distancing was a novel behavior specifically prescribed as an NPI for mitigating the impact of the COVID-19 pandemic; unlike handwashing, participants would not have engaged in this behavior prior to the pandemic, so there was no need to control for baseline differences between participants in their pre-pandemic frequencies of social distancing. For these reasons, we focused specifically on the NPI of social distancing.

RESULTS

All analyses were conducted using IBM Statistical Package for Social Sciences (SPSS) (Version 27). The statistical significance threshold was set at $p < 0.05$. Shapiro-Wilk tests revealed that participants' self-reported adherence ($p < 0.001$), anticipated shame for non-adherence ($p < 0.001$), perceptions of the moral wrongness of non-adherence ($p < 0.001$), and perceptions of disease severity ($p < 0.001$) all violated the assumption of normality. We therefore used Kendall's τ for all bivariate correlational analyses.

Do People Mimic Norms During a Pandemic?

The central hypothesis of the study, Hypothesis 1, was that people match their behavior to perceived social norms. If this is correct, then participants' current adherence to social distancing guidelines should be positively associated with their perceptions of others' adherence (Prediction 1.0). In support of this hypothesis, there was a positive association between people's perceptions of others' adherence to social distancing recommendations (M = 53.74, SD = 25.42) and their own adherence (M = 5.19, SD = 1.85), $\tau = 0.40$, $p < 0.001$, two-tailed, N = 149.

Do People Mimic Norms Due to the Threat of Social Exclusion?

Hypothesis 1.1 was that people follow norms out of concerns about exclusion or ostracism. If this is correct, then there should be positive associations (1) between participants' perceptions of social norms and their anticipated shame for non-adherence (Prediction 1.1.1), as well as (2) between participants' anticipated shame and their self-reported adherence (Prediction 1.1.2).

Self-reported adherence was positively linked to anticipated shame (M = 4.85, SD = 1.83), $\tau = 0.33$, $p < 0.001$, two-tailed, N = 147, but there was no relationship between anticipated shame and perceptions of social norms, $\tau = 0.09$, $p = 0.12$, two-tailed, N = 147. Collectively, this suggests that people's adherence may be motivated by a desire to avoid the feeling of shame, but this feeling of shame is independent of violation of perceived social norms.

Do People Use Normative Behavior to Gauge What Is "Moral"?

Hypothesis 1.2 was that people might use social norms to gauge what is moral. If this is correct, then there should be positive associations (1) between participants' perceptions of others' adherence and perceptions of the moral wrongness of non-adherence (Prediction 1.2.1), as well as (2) between participants' perceptions of the moral wrongness of non-adherence and their self-reported adherence (Prediction 1.2.2).

The findings with respect to morality parallel those observed for shame. There was a positive association between participants' self-reported adherence and their perceptions of the moral wrongness of non-adherence (M = 4.80, SD = 1.82), $\tau = 0.28$, $p < 0.001$, two-tailed, N = 148, but there was no association between participants' perceptions of the moral wrongness of non-adherence and their perceptions of others' adherence, $\tau = 0.08$, $p = 0.18$, two-tailed, N = 148. This suggests that people's adherence may be motivated by perceptions of morality, but these perceptions do not appear to be related to what other people are doing.

Do People Use Other People's Behavior as an Indicator of Disease Severity?

Hypothesis 1.3 was that people use others' behavior as an informative cue to the seriousness of the disease. If this is correct, then there should be associations (1) between participants' perceptions of others' adherence and their perception of the severity of COVID-19 (Prediction 1.3.1), as well as (2) between participants' perception of the severity of COVID-19 and their own adherence (Prediction 1.3.2).

Both results were consistent with this hypothesis. Participants' perceptions of others' adherence were positively associated with their perceptions of the seriousness of COVID-19 (M = 5.62, SD = 1.76), $\tau = 0.19$, $p = 0.001$, two-tailed, N = 148, which were positively associated with participants' own reported adherence levels, $\tau = 0.36$, $p < 0.001$, two-tailed, N = 148. This suggests that people's adherence is partially motivated by their perception of how serious COVID-19 is, a perception that itself is derived partly from observing others' behavior.

Mediating Effects of Shame, Moral Wrongness, and Disease Severity

These bivariate analyses lend support to Hypotheses 1 and 1.3. First, people's adherence to social distancing guidelines track their perceptions of others' adherence, supporting Hypothesis 1. Second, supporting Hypothesis 1.3, people appear to use others' behavior as an indicator of the severity of the disease, and therefore as a guide for their own behavior.

These results suggest that the effect of norms on adherence may be mediated by perceptions of disease severity. However, bivariate correlational analyses cannot directly address mediation. Moreover, we observed multiple inter-correlations between potential mediators (see **Figure 2**, which displays all bivariate relationships between all study variables of interest).

To more directly examine mediation and produce estimates of the direct and indirect effects of perceived social norms on adherence, we conducted mediation analyses using Hayes (2017) PROCESS macro for SPSS. To control for the observed statistical overlap between the potential mediators (**Figure 2**) and thereby isolate their independent effects, we included all mediators concurrently (as illustrated in **Figure 1**)[1] and used a

[1]We implemented this using Model 4 in PROCESS with participant adherence as the criterion, perception of others' adherence as the predictor, and anticipated shame, perceived moral wrongness of non-adherence, and perceived disease severity as mediators.

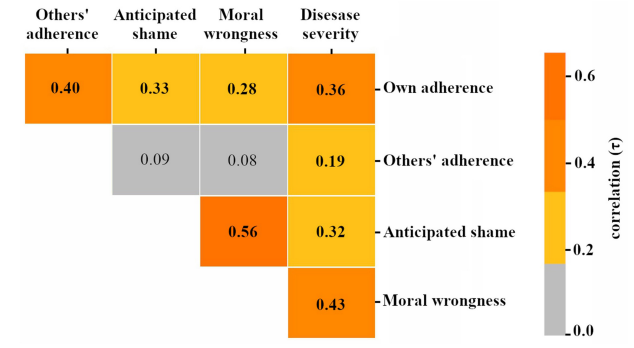

FIGURE 2 | Bivariate correlations between study variables of interest. Note: gray cells indicate non-significant ($p > 0.05$) correlations. All colored cells indicate significant ($p < 0.05$) correlations.

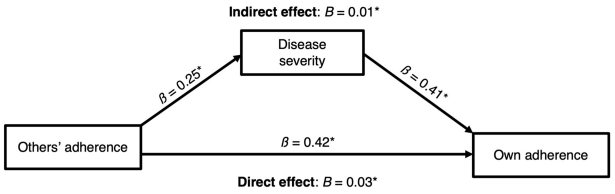

FIGURE 3 | Final mediation model with direct and indirect effects of perceived norms on adherence. *$p < 0.05$.

backward stepwise approach to determine the final model. All analyses employed a 95% CI and 5000 bootstrap as recommended by Hayes (2009). Our final sample size was sufficient to detect a moderate effect following SPSS PROCESS bias-corrected bootstrapping (Fritz and Mackinnon, 2007).

This procedure resulted in a final model (**Figure 3**) that included a significant indirect effect of norms on adherence through perceptions of disease severity, $ab = 0.007$, $SE = 0.003$, 95% BootCI [0.002, 0.014], as well as a direct effect of norms on adherence, $B = 0.031$, $SE = 0.005$, 95% CI [0.021, 0.040] (indirect effect VAF = 0.18).

Alternative Mediation Model

In our *a priori* model (**Figure 1**), we conceptualized the mediators (anticipated shame, perceptions of moral wrongness, and perceptions of disease severity) as *alternative* mediating pathways. However, one potential alternative would be for these psychological variables to have a serial relationship. Here, we describe and test this model. In the serial processing model, people could use others' adherence as an indicator of the magnitude of disease threat. High levels of adherence among others would cue high levels of disease severity, which would indicate that one could cause great harm to others by not adhering. Because non-adherence could cause such harm to others, moral cognitive systems could produce the perception that non-adherence is immoral or wrong[2]. In turn, the perception that non-adherence is morally wrong—and therefore likely to be met by devaluation from others—could activate the shame program. The shame program would then produce high levels of anticipated shame for non-adherence and thereby motivate adherence.

We tested this alternative model but did not find support for serial mediation (**Figure 4**). Specifically, the indirect effect of norms on adherence via the serial pathway through perceptions of disease severity, perceptions of moral wrongness for non-adherence, and anticipated shame for non-adherence was not

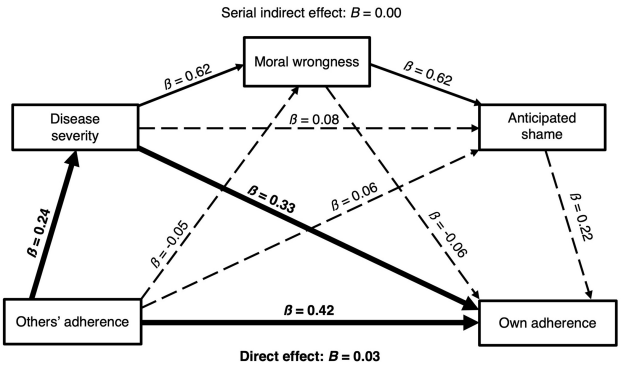

FIGURE 4 | Alternative serial mediation model. Solid lines indicate significant ($p < 0.05$) coefficients. Dashed lines indicate non-significant coefficients. Bolded lines indicate the significant pathways to individuals' adherence to social distancing guidelines.

significant ($a_1d_{21}d_{32}b_3 = 0.0015$, $SE = 0.0010$, 95% BootCI [-0.0001, 0.0040]). In fact, among the seven indirect pathways in this model from people's perceptions of others' adherence to their own adherence, only one exhibited a significant effect: the pathway from perceived norms to adherence through perceptions of disease severity—precisely the effect we observed in our *a priori* model (**Figure 4**).

We recognize that there may be other possible alternative models as well. However, thus far we have tested two conceptually sound models, and have found support for only one mediating pathway, which remained robust across both the *a priori* model and the alternative model: from perceived norms to adherence through perceptions of disease severity.

DISCUSSION

This study addressed two main questions: first, do people conform their social distancing behavior to what they think others are doing? The answer appears to be yes. Second, why do they do this? We tested several processes by which this might occur and found that people seem to perceive others' behavior as an informative cue to disease severity, and this in turn influences the extent to which they conform to public health guidelines.

Threat of Devaluation Does Not Appear to Explain the Relationship Between Norms and Adherence

Our findings indicated a relationship between people's adherence and their anticipated shame for non-adherence, but no relationship between participants' anticipated shame and their perceptions of social norms. These findings suggest that the emotion of shame may motivate adherence, but that we do not calibrate shame to our perceptions of others' adherence. These results tentatively falsify Hypothesis 1.1; the threat of social exclusion or ostracism does not appear to explain the relationship between social norms and people's adherence.

[2]We encourage the interested reader to consult Krasnow (2017), who discusses the distinction between "inward-facing" and "outward-facing" moral mechanisms. In the serial mediation model, both inward-facing (i.e., designed to regulate one's own behavior) and outward-facing (i.e., designed to regulate others' behavior) facets of moral cognition may come into play. In this model, moral cognition regulates one's own behavior—individuals may perceive non-adherence to risk harm to others, resulting in judgments of moral wrongness for non-adherence and thereby motivating adherence. However, this inward-facing function may itself be at least partly in the service of the outward-facing function of regulating others' behavior: these judgments of moral wrongness may activate the shame program, whose principal function is to avoid and mitigate the costs of devaluation by others.

Perceptions of Moral Wrongness Do Not Appear to Explain the Relationship Between Norms and Adherence

We observed a link between people's perceptions of the moral wrongness of non-adherence and their own adherence (Prediction 1.2.2), but there was no relationship between people's perceptions of social norms and their judgments of the moral wrongness of non-adherence (Prediction 1.2.1). This suggests that perceptions of what is morally right may motivate people to follow social distancing guidelines, but people's perceptions of the moral wrongness of non-adherence do not appear to be based on what others are doing (or not doing). These results tentatively falsify Hypothesis 1.2.

Learning About Disease Severity Through the Actions of Others

Study findings were consistent with all three predictions generated from Hypothesis 1.3, providing preliminary evidence that people use others' behavior as a cue to disease severity, and, in turn, as a guide for their own behavior.

However, perceived disease severity only partially mediated the relationship between participants' perception of social norms and their adherence. This means that more remains to be discovered about the association between perceived social norms and NPI adherence.

Explanations and Alternative Interpretations of Study Findings

The current study offers preliminary findings suggesting that perceived social norms may play an important role in people's psychological and behavioral responses to a pandemic, and therefore need to be better understood in order to mitigate the impact of epidemics and pandemics. Nonetheless, these results should be interpreted tentatively, as the current study had several limitations that should be addressed in future research.

Why Is Shame Not Linked to Social Norms?

The finding that shame for non-adherence was unrelated to perceived social norms does not appear to conform to the existing literature (e.g., Sznycer et al., 2016, 2018; Sznycer, 2019). One possibility is that anticipated shame was not an appropriate operationalization of concern about social devaluation. However, our anticipated shame measure was virtually identical to that used in research that showed a high degree of correspondence between shame and social devaluation in both a Western (Sznycer et al., 2016) and a large cross-cultural sample of small-scale societies (Sznycer et al., 2018). One possible explanation for the apparent discrepancy between the current study and previous literature is that the latter used evolutionarily relevant (and non-novel) behaviors, whereas we focused on the behavior of social distancing, which—at least in its very precisely prescribed sense—exhibits evolutionarily novel features. Although ancestral humans likely had behavioral strategies for pathogen avoidance that involved physical distancing, it is less plausible that there would have been precisely specified distances associated with such behavior, which contrasts with formal guidelines during the COVID-19 pandemic (e.g., to maintain a distance of at least 1.5 m from others). It is unlikely that our minds evolved to perceive a meaningful difference between (a) an individual approaching another and stopping at a distance of 1.6 m, and (b) an individual approaching another and stopping at a distance of 1.4 m. These behaviors would have been virtually identical, in function, in ancestral environments, and it is unlikely that selection would have shaped the human mind to perceive them as being substantively different—despite one of them being considered adherence to, and the other a violation of, COVID-19 social distancing guidelines.

Why Are Perceptions of Morality Not Linked to Social Norms?

A similar line of reasoning may help explain the absence of a relationship between perceived norms and perceptions of the moral wrongness of non-adherence. Moreover, behaviors that spread COVID-19, such as not socially distancing, appear to lack the properties that activate disease-avoidance systems (Ackerman et al., 2018; Seitz et al., 2020) or trigger automatic emotional reactions, which can be important drivers of moral judgment (Greene, 2001).

COVID-19 is abstract, invisible to the naked eye, and seemingly disconnected from the actions that proliferate it. We do not see or feel the moment COVID-19 transmits from one person to another, and by the time symptoms start showing—if they manifest at all; infected individuals can be contagious without exhibiting any symptoms (see Cheng et al., 2020; Huff and Singh, 2020; Tindale et al., 2020)—the person who spread the virus is often far away and several days have passed since the infection event (Varella et al., 2021). Not only is disease transmission not directly observable, but cues that our mind is likely to process as increasing the risk of transmission, such as physical contact or coughing, are not required for transmission to occur. These properties of the disease and its transmission may make it harder for non-adherent behaviors to trigger moral judgment and condemnation.

Intention also plays an essential role in moral judgment; if a moral transgression is unintentional, it is typically judged much less harshly than intentional transgressions (DeScioli et al., 2011; DeScioli and Kurzban, 2013; Guglielmo, 2015). Because it is not easy to discern whether someone coming within 1.5 meters of someone else represents an intentional transgression, many behaviors that reflect COVID-19 non-adherence may lack the features of the type of intentional transgression to which human moral systems are attuned.

Limitations on Study Design and Future Research

Our study design had several limitations that should be addressed by future research.

Single-Item Measures

Because the study survey assessed a diverse set of constructs (e.g., perceptions of others' adherence, own adherence, anticipated shame for non-adherence, moral wrongness of non-adherence)

for multiple scenarios, it was not feasible to use a lengthy measure for each construct for each scenario; doing so would have resulted in a long and unwieldy survey that induced participant fatigue and attrition. Previous research on several of the central constructs of interest has employed a similar design: a single-item measure of the construct for each scenario (e.g., Sznycer et al., 2018's cross-cultural research on shame, DeScioli et al., 2011's research on moral wrongness). Although some work (e.g., Loo, 2002) has expressed concerns about the psychometric validity of single-item scales, the items used in the current study exhibit high face validity, and multiple studies have empirically demonstrated that single-item scales tap the same construct as their lengthier counterparts (see Gardner et al., 1998; Yarkoni, 2010; Konstabel et al., 2017). Moreover, the ability of single items to tap the same construct as multi-item measures has not just been observed generally, but for shame specifically: the mean item-total correlations for multiple subscales of the Guilt and Shame Proneness scale (Cohen et al., 2011) exceed 0.70, indicating that any of several individual items would be psychometrically valid substitutes for longer scales (data available at https://osf.io/3wf4a/). In short, the single-item measures that we used followed precedents in the relevant literature, exhibited high face validity, and tapped constructs that specifically have been shown to be validly assessable via individual items. Nonetheless, further studies on the phenomena and relationships observed in the current study would benefit from employing longer measures with demonstrated psychometric validity, especially when researchers can afford the increased questionnaire length.

Generalizing Study Findings to a Global Scale

The current study's sample was drawn exclusively from Australia. This may limit the cross-cultural generalizability of study findings. Australia's relatively "loose" individualistic culture, for example, may offer a proximate explanation for the absence of a link between perceived social norms and anticipated shame for non-adherence. A pattern similar to one observed in the current study was recently observed in a set of studies based out of the Netherlands—a nation with a very "loose" culture (Gelfand et al., 2021). In these Netherlands-based studies, participants (N = 1142) did not increase conformity in response to high perceived pathogenic infection risk (van Leeuwen and Petersen, 2021). This contrasts with countries like Japan, which is a collectivist, tight culture in which people value norms of prosocial cooperation and are unlikely to engage in behavior that could result in ostracism (Böhm et al., 2016). In the context of the COVID-19 pandemic, nations with higher levels of cultural tightness had approximately 5 times fewer cases compared to countries with comparatively higher levels of cultural looseness (see Gelfand et al., 2021). This important proximate role of cultural tightness-looseness on COVID-19-related outcomes highlights the need for future work to investigate cross-cultural similarities and differences in the predictors of NPI adherence.

Individual Differences

Future work should also investigate the role of individual differences as predictors of adherence to NPIs. For example, slow life history strategists are characterized by a propensity to long-term planning and risk aversion (Del Giudice and Belsky, 2011). Consistent with this, individuals who pursue a slower life history strategy exhibit greater adherence to COVID-19 precautions (Corpuz et al., 2020). Theory and evidence also suggest that differential selection pressures shaped higher pathogen disgust and greater health-related concern in women relative to men (see Al-Shawaf and Lewis, 2013; Al-Shawaf et al., 2018; Luoto and Varella, 2021). Such differences may orient women to engage in a more cautious approach toward COVID-19 than men and be associated with sex differences in attitudes toward protective behaviors and adherence to NPIs (Dinić and Bodroža, 2021; Luoto and Varella, 2021). Given these important roles of individual differences in the context of the COVID-19 pandemic, future research should incorporate these and other individual differences into their investigations of adherence to NPIs (see Varella et al., 2021; see also Tybur et al., 2016). We also encourage the interested reader to consult evolutionary literature on why individuals in different phenotypic condition are expected to exhibit different responses to the same environmental inputs (e.g., Lewis, 2015; Lewis et al., 2018, 2020a,b; Lukaszewski et al., 2020).

Other NPIs

The analyses presented in the current study cannot address the issue of non-adherence to quarantine measures. As breaches of quarantine constitute a significant infection risk and have been frequently reported, future research is needed to understand the reasons why people do or do not follow quarantine protocols. One challenge that such research will face is that only a small proportion of the population is actually advised to quarantine. This presents a measurement challenge, as people who have not been advised to quarantine may report their current adherence as high (i.e., "I would quarantine if I had to") or low (i.e., "I haven't had COVID, so I haven't quarantined") depending on their interpretation of the question. To address this methodological challenge, future research could specifically target members of the population who are known to have had experience with quarantine.

Do Perceived Norms Actually Influence Adherence?

Because the present study was correlational, we cannot infer with certainty the causal direction, if any, of the observed relationship between perceived social norms and participants' self-reported adherence. One possibility is that people simply associate with others who engage in similar behaviors, but are not actually influenced by others' behavior. This alternative account would be plausible if participants considered just their own interpersonal milieu when answering questions about others' adherence. However, the question we asked was: "What percentage of people *in your country* do you think follow the recommendations below?" [emphasis added]. The wording of the question was designed to prompt participants to consider a much larger reference group than just their immediate social circle. Nonetheless, there is research to suggest that individuals may exhibit an in-group bias in the context of

pathogen risk wherein they disproportionately direct attention to and weight the actions of members of their in-group (see Navarrete and Fessler, 2006; see also Thornhill and Fincher, 2014). We therefore cannot conclusively rule out the possibility that participants used, as a reference group, just those individuals with whom they associate, despite being explicitly instructed to use country-wide levels of adherence as the point of reference.

Another possibility is that the statistical association between participants' perceptions of others' adherence and their own self-reported adherence resulted from participants engaging in socially desirable responding wherein they matched their own *reported* levels of adherence to their perceptions of others' adherence. Those participants who perceived others as showing greater adherence may have had the greatest incentive to self-report similarly high levels of adherence, whereas participants who perceived others to not be adhering would have had less incentive to self-report high levels of adherence. Such socially desirable responding could lead to a statistical association between participants' self-reported adherence and their perceptions of others' adherence. However, this account does not appear to easily explain either (1) the relationship observed between perceived norms and perceptions of disease severity or (2) the indirect effect observed in the mediation model (and replicated in the alternative serial mediation model). This suggests that although socially desirable responding may have occurred in this study, it cannot account for the overall pattern of findings. Future studies using self-report measures of adherence to NPIs would nonetheless benefit from including a social desirability scale to control for socially desirable responding (Larson, 2019). More broadly, future research—especially experimental designs that manipulate perceived social norms—is needed to more conclusively establish the influence of social norms on adherence to public health measures during a pandemic.

Implications of the Present Study

The findings from the present study, although preliminary, could have considerable implications in the ongoing fight against COVID-19 and future pandemics. The current findings suggest that public messaging campaigns designed to promote adherence to NPIs are more likely to be effective when they focus on "leading by example," or what social psychologists have sometimes referred to as "social proof" (Cialdini, 2009). This also points toward the critical role that political leaders may play in fighting the pandemic—not just through their policy content and mandates (Luoto and Varella, 2021; Priesemann et al., 2021), but through their behaviors on display for the public eye. If, as the current study suggests, people use others' behavior as an informative cue to the seriousness of the pandemic, then the behavior of political leaders, social influencers, and social movements—which are widely disseminated on public television and social media—may have a profound influence on people's perception of the pandemic and, crucially, the actions they take in response to it (see also Haslam et al., 2021, for a discussion of the top-down influence of leader identity).

It is worth stressing the importance of this point. If the findings of the current study are robust, to act in the opposite way (i.e., modeling non-adherent behavior) could have the detrimental effect of promoting the flouting of NPI guidelines. If so, it is paramount that individuals with influence in the public sphere be mindful of the role of their own publicly observable behavior in combating pandemics.

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://osf.io/nsf2p/?view_only=b54137011201471aaebd857f47f57a19.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Murdoch University Human Research Ethics Committee. The online survey explicitly asked participants for their consent to participate; participants were not allowed to access the study survey unless they clicked on a "Yes" button to indicate their consent to participate.

AUTHOR CONTRIBUTIONS

JN: conceptualization, writing—original draft, reviewing and editing, and visualization. KE: conceptualization, methodology, and data collection. AS: conceptualization and methodology. LA-S: conceptualization, methodology, and manuscript preparation. DL: conceptualization, supervision, writing—reviewing and editing. All authors contributed to the article and approved the submitted version.

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