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Ecological Drivers of Non-kin Cooperation in the Hymenoptera

Madeleine M. Ostwald[1]*, Brian R. Haney[2] and Jennifer H. Fewell[1]

[1] School of Life Sciences, Arizona State University, Tempe, AZ, United States, [2] Division of Natural Sciences, College of Mount Saint Vincent, Riverdale, NY, United States

Despite the prominence of kin selection as a framework for understanding the evolution of sociality, many animal groups are comprised of unrelated individuals. These non-kin systems provide valuable models that can illuminate drivers of social evolution beyond indirect fitness benefits. Within the Hymenoptera, whose highly related eusocial groups have long been cornerstones of kin selection theory, groups may form even when indirect fitness benefits for helpers are low or absent. These non-kin groups are widespread and abundant, yet have received relatively little attention. We review the diversity and organization of non-kin sociality across the Hymenoptera, particularly among the communal bees and polygynous ants and wasps. Further, we discuss common drivers of sociality across these groups, with a particular focus on ecological factors. Ecological contexts that favor non-kin sociality include those dominated by resource scarcity or competition, climatic stressors, predation and parasitism, and/or physiological constraints associated with reproduction and resource exploitation. Finally, we situate Hymenopteran non-kin sociality within a broader biological context by extending insights from these systems across diverse taxa, especially the social vertebrates. Non-kin social groups thus provide unique demonstrations of the importance of ecological factors in mediating the evolutionary transition from solitary to group living.

Keywords: social evolution, relatedness, kinship, wasps, bees, ants

Edited by:
Floria M. K. Uy,
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Reviewed by:
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Alessandro Cini,
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United Kingdom

***Correspondence:**
Madeleine M. Ostwald
ostwald.madeleine@gmail.com

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INTRODUCTION

Social animals represent some of the most ubiquitous and ecologically dominant organisms globally (Hölldobler and Wilson, 1990; Krause and Ruxton, 2002; Ward and Webster, 2016). To date, our understanding of how social groups emerge has been rooted overwhelmingly in the study of family groups. From these groups have emerged useful theoretical frameworks for explaining cooperation in nature, especially kin selection theory, which posits that indirect fitness benefits of helping kin can compensate for direct fitness costs (Hamilton, 1964; West-Eberhard, 1975; Trivers and Hare, 1976; Abbot et al., 2011; Bourke, 2014). Nevertheless, many animals form groups with non-relatives, and in these societies direct fitness gains are generally the major component of inclusive fitness (Clements and Stephens, 1995; Dugatkin, 2002; Goodnight, 2005; Clutton-Brock, 2009; Queller, 2011). These social groups, which exist across diverse animal taxa

(Bernasconi and Strassmann, 1999; Clutton-Brock, 2009; Riehl, 2013; Wilkinson et al., 2016; Brask et al., 2019; Suarez and Goodisman, 2021), demonstrate the value of examining the diversity of selection contexts for understanding the evolution of sociality, and provide useful models for examining ecological drivers of social evolution.

Kin selection has proven critically valuable for understanding the evolution of eusociality, especially within the highly related colonies of the social insects (West-Eberhard, 1975; Queller and Strassmann, 1998; Hughes et al., 2008; Abbot et al., 2011; Bourke, 2011; Linksvayer and Wade, 2011). However, eusociality is rare; even among the Hymenoptera; other forms of group living are considerably more common (Heinze et al., 2017; Hunt and Toth, 2017; Wcislo and Fewell, 2017; Fewell and Abbot, 2018). Perhaps due to the prominence of kin selection as a framework for understanding insect sociality, non-kin groups in insects have received relatively little attention, despite advances in our understanding of non-kin vertebrate groups (Clutton-Brock, 2009; Riehl, 2013; Wilkinson et al., 2016; Brask et al., 2019). Departures from a kin-centric framework for understanding insect social evolution may enable valuable connections to other animal groups, contributing to a broader body of evolutionary theory. Further, these systems may be neglected because interactions among non-kin rarely (if ever) constitute altruism—that is, behavior that reduces the fitness of the actor and increases the fitness of the group—which has been a major focus of social evolutionary research in the eusocial Hymenoptera (Hamilton, 1972; Simon, 1990; Foster et al., 2006; Kennedy et al., 2018). Rather, non-kin associations provide examples of cooperation based on mutual benefits of grouping, with or without reproductive division of labor.

We review advances in our understanding of non-kin social groups in the Hymenoptera, with a focus on patterns of diversity in social structure and ecological context. We characterize variation in the organization of these groups and describe the distribution of non-kin sociality across the bees, ants, and wasps. Across these groups, we then highlight common ecological drivers of non-kin sociality, particularly environmental challenges and intra- and inter-specific interactions. Finally, we synthesize insights from the current body of research on non-kin sociality and highlight promising directions for future research. In doing so, we emphasize the role of ecological context in shaping sociality at its evolutionary origins.

NON-KIN COOPERATION IN THE HYMENOPTERA

Non-kin sociality is found broadly among the social ants, wasps, and bees, and ranges in complexity from simple, facultative nest sharing in primarily solitary populations to cooperative founding of eusocial colonies (**Figure 1**). For the purposes of this review, we define sociality as any long-term association between conspecifics characterized by mutual tolerance and/or cooperation within shared nesting space (Costa, 2006; Fewell and Abbot, 2018). By "long-term," we refer to an extended or significant portion of an individual's lifespan, as opposed to more transient interactions like mating. Further, we emphasize mutual tolerance as a minimum requirement in our definition of sociality for the sake of including even groups characterized by limited cooperative behavior. Mutual tolerance serves as a preadaptation for the evolution of cooperation, by enabling individuals to share nest space and providing opportunities for more complex social interactions (Michener, 1974, 1990a).

Specifically, we examine social interactions in the context of breeding and offspring care, because behavioral decisions in these contexts have important fitness impacts. We emphasize nest sharing to exclude from our definition of sociality those animals living within aggregations of spatially clustered nests, but otherwise living solitarily. Though some Hymenoptera (such as army ants) are non-nesting, nests are used predominantly by this taxon as an essential physical site for the prolonged interactions intrinsic to social living. Additionally, we define sociality as distinct from intraspecific social parasitism, and therefore exclude from our discussion those systems in which non-kin relationships arise through parasitic behavior (Beekman and Oldroyd, 2008), including adoption of unrelated offspring (Klahn, 1988; Nonacs and Reeve, 1993) and cleptoparasitism (Michener, 1974; Rozen, 1991).

Non-kin associations vary considerably in the degree of cooperation, and thus serve as an important counterpoint to vertebrate sociality. However, discussions of cooperation for social insects and social vertebrates have historically been treated separately. For example, cooperation in the social insects is often studied in the context of task allocation and division of labor (Hölldobler and Wilson, 1990; Seeley, 1996; Beshers and Fewell, 2001), while social vertebrate sociality is more often discussed in terms of the costs and benefits of cooperative interactions (Hamilton, 1964; Dugatkin, 2002; Clutton-Brock, 2009). Defining cooperation itself has also presented challenges, with debate surrounding the questions of whether cooperative interactions may incur differential costs for actor and recipient, and whether cooperative sociality can be maintained under such conditions without indirect fitness gains (Lehmann and Keller, 2006; West et al., 2006, 2007; Bergmüller et al., 2009). Within such discussions, however, has emerged a central theme that cooperation broadly entails behaviors that benefit the social group (Clutton-Brock, 2009).

Social Evolution in the Hymenoptera

The evolution of cooperative behaviors is shaped by ecological context and by the phylogenetic pathway that group has taken to sociality. The task of categorizing the various forms of sociality and their evolutionary histories has been the subject of considerable debate (Wilson, 1971; Michener, 1974; Crespi and Yanega, 1995; Toth et al., 2016; Boomsma and Gawne, 2018; Richards, 2019). A well-established hypothesis has proposed a stepwise evolutionary progression from simple forms of sociality to complex eusociality (Evans, 1956; Wilson, 1971; Evans and West-Eberhard, 1973; Rehan and Toth, 2015). Recent, renewed discussion of this topic has challenged the theoretical presumption of a "social ladder" in which less complex social forms represent intermediate "levels" along an evolutionary trajectory toward eusociality (Linksvayer and Johnson, 2019;

FIGURE 1 | Examples of non-kin sociality are widespread across hymenopteran taxa. In the ants, unrelated foundresses may cooperate to rear eusocial colonies, as in the harvester ant *Pogonomyrmex californicus* (top left; photo by Elizabeth Cash). Similarly, foundresses of some wasp species, like the paper wasp *Polistes dominula* (bottom; photo by Meagan Simons), may cooperatively found eusocial nests with non-relatives. Non-kin associations are also found among the communal bees, such as the sweat bee *Agapostemon virescens* (top right; photo by Nicholas Dorian), which shares nest-entrance guarding duties with unrelated nestmates.

Holland and Bloch, 2020). Accordingly, we consider the diversity of cooperative systems in the social insects not as transitional forms in the evolution of sociality, but instead in terms of their shared cooperative behavioral repertoires that are adaptive in a given ecological context.

One of the simplest forms of sociality, known as communal living, refers to societies in which multiple same-generation females (often unrelated) share nesting space but independently forage and provision their own offspring (Michener, 1974). Communal groups are characteristically casteless: group members are not distinguished behaviorally or morphologically by their capacity for reproduction. Only a subset of tasks—typically nest construction and nest defense—are shared cooperatively. Communal groups often exist among otherwise solitary populations of bees and wasps, and are characterized by behavioral repertoires similar to those of solitary females: they mass-provision brood at the egg stage, and do not engage in further direct parental care (Wcislo and Tierney, 2009; Wcislo and Fewell, 2017). In contrast, other social insects, including ants, wasps, and some bee taxa, perform direct parental care in which larvae are fed progressively (Field, 2005). The cooperative repertoire of these groups is similarly expanded. These associations occur when related or unrelated females found nests cooperatively (pleometrosis) by sharing or dividing such tasks as provisioning, nest construction, and defense (Ross and Matthews, 1991; Heinze et al., 2017).

Social Diversity in the Hymenoptera

Here we describe the diversity of non-kin sociality defined as long-term adult nest sharing, with groups often characterized by cooperative behaviors and task sharing. Because relatedness is a relative attribute (Pamilo, 1989), we do not strictly define kin vs. non-kin, but rather focus on groups in which individuals may be no more related to their nestmates than they are to non-nestmates. For some of the systems we discuss, non-kinship in social groups has been evaluated with high confidence by inferring relatedness from molecular markers. In many other cases, the presence of non-relatives in social groups has been inferred from observations of nest-joining behavior, often by individuals from distant nests (in bees and wasps), or of cooperative nest founding by presumed unrelated foundresses (in wasps and ants). Though these observations cannot confirm the degree of relatedness between joiners and their nestmates, they provide suggestions of potential flexibility in tolerance toward unrelated conspecifics. Because the data on kinship in these groups is so incomplete, we highlight these uncertain cases as promising avenues for future genetic investigation.

Within the Hymenoptera, we explore non-kin groups among wasps, bees, and ants, finding limited evidence for true sociality among the sawflies (Hymenoptera: Symphyta), which have short adult lifespans and are non-nesting (Kudo et al., 1998). For each group, we describe patterns and diversity of non-kin social systems. We do not present an exhaustive review of all known non-kin groups in the Hymenoptera, but instead highlight common patterns of social organization across the major suborders.

Wasps: Communal Societies and Foundress Associations

The wasps (Hymenoptera: Apocrita) comprise more than 37 families, among which only three (Aculeata: Pompilidae, Sphecidae, and Vespidae) contain social species (Hunt and Toth, 2017). Non-kin groups are found within all three of these families (**Table 1**). Communal nesting has been described for several species, and among these, nest-joining by non-relatives is possible, though unconfirmed, for the spider wasp *Auplopus semialatus* (Pompilidae: Pepsinae); (Wcislo et al., 1988), the digger wasp *Crabro cribrellifer* (Crabronidae: Crabroninae); (Wcislo et al., 1985), and the pollen wasp *Trimeria howardii* (Vespidae: Masarinae); (Zucchi et al., 1976). Facultative nest sharing is likewise known among the hover wasps (Vespidae: Stenogastrinae), where unrelated females can join established foundresses (Strassmann et al., 1994; Turillazzi, 2012). Similarly, among the primitively eusocial paper wasps (Vespidae: Polistinae), foundress associations often form among sisters or other close relatives (West-Eberhard, 1969; Ross and Matthews, 1991), but in many cases may be comprised of non-kin (Queller et al., 2000; Hunt, 2007; Mora-Kepfer, 2014). For the paper wasp *Polistes dominula*, 15–35% of foundress associations consist of unrelated females (Queller et al., 2000; Zanette and Field, 2008; Leadbeater et al., 2011). Co-founding by non-relatives is also known, but uncommon, in *Polistes fuscatus* (Klahn, 1979) and *Polistes exclamans* (MacCormack, 1982). Unlike communal groups, these societies are characterized by high reproductive skew, so unrelated joiners often become subordinate helpers with limited reproductive opportunities (Queller et al., 2000; Leadbeater et al., 2010; Mora-Kepfer, 2014).

Bees: Communal and Parasocial Societies

Communal nesting occurs across all six major bee families (Wcislo, 1993; Kukuk et al., 2005), and many of these communal groups are known or expected to consist of non-kin. This social strategy is perhaps best known among the sweat bees (Halictidae), which are known for their incredible diversity of social behaviors (Michener, 1974, 1990b, 2007; Brady et al., 2006). Halictid communal nesting has been described within the subfamilies Halictinae and Nomiinae; for most of these species, relatedness among communal nestmates is unknown (Michener, 1969; Wcislo, 1993; Vogel and Kukuk, 1994; Wcislo and Engel, 1996), but may be inferred to be low through observations of nest-joining behavior (Michener and Lange, 1958; Abrams and Eickwort, 1981; Richards et al., 2003). Kukuk and Sage analyzed two polymorphic genetic loci among colonies of the sweat bee *Lasioglossum hemichalceum* (Halictidae: Halictinae) and found relatedness within reproductively active nests to be indistinguishable from zero (1994). Communal nesting is present but less common among the Colletid bees (Sakagami and Zucchi, 1978), with low relatedness ($r = 0.26$) confirmed among nestmates of *Amphylaeus morosus* (Colletidae: Hylaeinae) (Spessa et al., 2000). Similarly, non-kin nesting is possible among the communal Andrenidae (Danforth, 1991; Paxton et al., 1999), and has been confirmed for two species: *Andrena scotica* (formerly *jacobi*); (Andrenidae: Andreninae) (Paxton et al., 1996) and *Macrotera* (formerly *Perdita*) *texana* (Andrenidae: Panurginae) (Danforth et al., 1996).

In other cases, the social organization of some non-kin bee groups is more aptly described by the umbrella term “parasocial,” which includes all associations of same-generation adults, which may be cooperative or non-cooperative, and which may exhibit high or low reproductive skew (Michener, 1974). This is the case for many bees of the family Apidae, which includes both solitary and highly social species. For example, bees in the genus *Exomalopsis* (Apidae: Apinae) form multi-female nests, which may be characterized by cooperative provisioning (Michener, 1966) and even reproductive skew (Raw, 1977). Relatedness in this genus has not been formally investigated, but is likely to be low for many species, considering the high number of females per nest (884 in one nest of *E. aureopilosa*; Rozen, 1984). Non-kin associations could also be found among pleometrotic foundresses of eusocial colonies, though this is rare within the bees. Low relatedness has been described for co-foundresses of the primitively eusocial sweat bee *Halictus ligatus*, likely arising from chance encounters among females emerging from their winter hibernacula (Richards and Packer, 1998).

An interesting case of non-kin sociality exists among the large carpenter bees in the genus *Xylocopa* (Apidae: Xylocopinae). Nest-joining behavior has been observed in several species, in many cases by unrelated bees (Gerling, 1982; Gerling et al., 1983; Velthuis, 1987; Michener, 1990a; Hogendoorn and Leys, 1993; Peso and Richards, 2011). However, low relatedness in social groups has only been demonstrated with molecular evidence for two species, *X. sonorina* and *X. virginica* (Ostwald et al., 2021a, this issue; Vickruck and Richards, 2021, this issue). Sociality in these groups is not easily classified, given variation and ambiguity in helping behavior, reproductive skew, and generational overlap (Gerling et al., 1989; Michener, 1990a; Hogendoorn and Velthuis, 1993). In most cases, a single dominant female per social nest will monopolize egg laying and provisioning behavior, with nestmates potentially contributing to nest guarding (Gerling et al., 1983, 1989; Hogendoorn and Velthuis, 1999; Buchmann and Minckley, 2019).

Ants: Foundress Associations and Primary Polygyny

In the ants, non-kin sociality through pleometrosis is relatively commonplace in incipient colonies, but usually ends with a queen culling event triggered by worker emergence (Bernasconi and Strassmann, 1999). However, permanent non-kin social groups

TABLE 1 | Hymenopteran species with the strongest evidence for non-kin associations.

	Taxon	Social organization	Evidence for non-kin sociality	Within-group *r*	References
Wasps	Vespidae				
	Stenogastrinae				
	Liostenogaster flavolineata	Primitively eusocial	Allozyme analysis	Not reported for foundresses	Strassmann et al., 1994
	Polistinae				
	Mischocyttarus mexicanus	Primitively eusocial	Behavioral observations	NA	Mora-Kepfer, 2014
	Polistes exclamans	Primitively eusocial	Behavioral observations	NA	MacCormack, 1982
	Polistes fuscatus	Primitively eusocial	Behavioral observations	NA	Klahn, 1979
	Polistes dominula	Primitively eusocial	Microsatellite analysis	~0.1 (for 15% of population)	Queller et al., 2000; Zanette and Field, 2008
Bees	Andrenidae				
	Panurginae				
	Macrotera texana	Communal	DNA fingerprinting	0.008	Danforth et al., 1996
	Andreninae				
	Andrena scotica	Communal	Microsatellite analysis	~0	Paxton et al., 1996
	Halictidae				
	Halictinae				
	Lasioglossum hemichalceum	Communal	Allozyme analysis	0.07	Kukuk and Sage, 1994
	Halictus sexcinctus	Communal or primitively eusocial	Behavioral observations	NA	Richards et al., 2003
	Halictus ligatus	Primitively eusocial	Allozyme analysis	−0.18	Richards and Packer, 1998
	Agapostemon virescens	Communal	Behavioral observations	NA	Abrams and Eickwort, 1981
	Pseudagapostemon divaricatus	Communal	Behavioral observations	NA	Michener and Lange, 1958
	Colletidae				
	Hylaeinae				
	Amphylaeus morosus	Communal	Allozyme analysis	0.26	Spessa et al., 2000
	Apidae				
	Xylocopinae				
	Xylocopa virginica	Parasocial	Microsatellite analysis	0.09–0.30	Vickruck and Richards, 2021, this issue
	Xylocopa sonorina	Parasocial	Microsatellite analysis	−0.09–0.35	Ostwald et al., 2021a, this issue
	Xylocopa sulcatipes	Parasocial or semisocial	Behavioral observations	NA	Velthuis, 1987
	Xylocopa pubescens	Parasocial or semisocial	Behavioral observations	NA	Gerling et al., 1983; Hogendoorn and Leys, 1993
Ants	Formicidae				
	Myrmecinae				
	Atta texana	Eusocial	Behavioral observations	NA	Moser and Lewis, 1981
	Acromyrmex versicolor	Eusocial	Allozyme analysis	−0.12	Rissing et al., 1989
	Acromyrmex heyeri	Eusocial	Isozyme analysis	Not reported	Diehl et al., 2001
	Acromyrmex striati	Eusocial	Isozyme analysis	Not reported	Diehl et al., 2001
	Myrmica gallienii	Eusocial	Isozyme analysis	0.01	Seppä, 1996
	Pogonomyrmex californicus	Eusocial	Microsatellite analysis	0.059	Overson et al., 2016

(Continued)

TABLE 1 | (Continued)

Taxon	Social organization	Evidence for non-kin sociality	Within-group *r*	References
Messor pergandei	Eusocial	Microsatellite analysis	∼ 0	Helms and Helms Cahan, 2012
Camponotus ligniperdus	Eusocial	Microsatellite analysis; DNA fingerprinting	Not reported	Gadau et al., 1998
Formicinae				
Myrmecocystus mimicus	Eusocial	Microsatellite analysis	0.053	Eriksson et al., 2019
Formica podzolica	Eusocial	Microsatellite analysis	0.156	DeHeer and Herbers, 2004
Oecophylla smaragdina	Eusocial	Microsatellite analysis	0.08	Schlüns et al., 2009
Ponerinae				
Neoponera inversa	Eusocial	Microsatellite analysis	−0.036 (2007)	Heinze et al., 2001; Kolmer et al., 2002; Kellner et al., 2007
Neoponera villosa	Eusocial	Microsatellite analysis	0.024	Kellner et al., 2007
Myrmeciinae				
Myrmicia pilosula	Eusocial	Microsatellite analysis	0.088	Qian et al., 2012
Myrmicia rubra	Eusocial	Microsatellite analysis; Isozyme analysis	0.041 (1982)	Pearson, 1982, 1983; Seppä and Walin, 1996
Dolichonderinae				
Iridomyrmex purpureus	Eusocial	mtDNA analysis	Not reported	Carew et al., 1997

Where available, we report r-values for comparisons among adult female nestmates, often foundresses.

can form when a pleometrotic queen association extends past worker emergence and into colony maturity. This results in primary polygyny, a group of unrelated worker lineages that share a nest, colony resources, and colony tasks. Importantly, workers in polygynous colonies may be close kin if they were produced by the same queen. Nevertheless, overall worker nestmate relatedness is often low in polygynous colonies (DeHeer and Herbers, 2004; Kellner et al., 2007). More importantly, the queens themselves represent prominent examples of non-kin cooperative behavior, analogous to cooperative breeders in other taxa, regardless of offspring group relatedness. Primary polygyny is generally found interspersed between monogynous colonies or as the majority structure in discrete populations, but has never been documented as the only social structure of an ant species.

Primary polygyny is represented in several ant subfamilies but is especially well documented in the Myrmicinae. Moser and Lewis (1981) first observed multiple unrelated queens in mature colonies of the Texas leaf-cutter ant *Atta texana*. Mintzer and Vinson subsequently found that these cooperative associations are stable and beneficial to *A. texana* queen survival in the lab (Mintzer and Vinson, 1985; Mintzer, 1987). Shortly afterward, Rissing et al. (1989) utilized allozyme markers to directly show that cohabiting *Acromyrmex versicolor* queens were not related and also reared stable multi-queen colonies in the lab. There is also genetic evidence, using isoenzymes, that two South American Acromyrmex species practice primary polygyny, *A. striatus* and *A. heyeri* (Diehl et al., 2001). Multiple, unrelated queens were also found in colonies of *Myrmica gallienii* using enzyme electrophoresis (Seppä, 1996), however colony age was not reported in this study. Primary polygyny may also occur in the fungus growing ant species, *Cyphomyrmex transversus*. Multiple queens were found in 37.7% of colonies examined by Ramos-Lacau et al. (2012) but it is unknown if these queens were related. Within the Myrmicinae, there are also several harvester ant species that practice primary polygyny. *Pogonomyrmex californicus* displays primary polygyny in southern California, as confirmed with field observation (Johnson, 2004), laboratory colonies (Clark and Fewell, 2014; Overson et al., 2014), and microsatellite analysis (Overson et al., 2016). Primary polygyny also occurs in a California population of the seed harvester *Veromessor pergandei*, also confirmed using microsatellites (Helms and Helms Cahan, 2012). Queens of another species in the same genus, *Messor barbarous*, can be induced into stable cooperative associations in the lab, but no polygynous colonies have been found in the field (Provost and Cerdan, 1990).

Within the subfamily Formicinae, the honeypot ant *Myrmecosystus mimicus* also practices primary polygyny in an Arizona population as confirmed by microsatellite analysis by Hölldobler et al. (2011). The mound building ant *Formica podzolica* exhibits primary polygyny in Colorado, as suggested by field excavation (Deslippe and Savolainen, 1995) and confirmed through microsatellite analysis (DeHeer and Herbers, 2004). Finally, multiple unrelated queens have been found in mature colonies of the pleometrotic weaver ant *Oecophylla smaragdina*, strongly suggesting primary polygyny (Schlüns et al., 2009).

Some of the most detailed genetic and behavioral research has been performed on species in the Ponerinae subfamily. Primary polygyny has been confirmed in *Neoponera inversa* through behavioral observation in the field and lab (D'Ettorre et al., 2005) as well as with multiple microsatellite analyses (Heinze et al., 2001; Kolmer et al., 2002). In a closely related species, *Neoponera villosa*, queen cooperation has been demonstrated in the lab (Trunzer et al., 1998) and unrelated queens have been documented in field colonies (Kellner et al., 2007), strongly suggesting primary polygyny. Mature *Neoponera striata* Smith colonies have also been found with multiple queens, but more work is needed on queen relatedness to confirm primary polygyny (Rodrigues et al., 2011). The arboreal trap jaw ant *Odontomachus hastatus* has been found in colonies containing several queens and workers, but it is unknown if these queens are related (Oliveira et al., 2011).

Primary polygyny has also been confirmed via microsatellite analysis in two species of the Myrmeciinae: the Australian jumper ant *Myrmicia pilosula* (Qian et al., 2012) and the red ant *Myrmicia rubra* (Pearson, 1982, 1983; Seppä and Walin, 1996).

Finally, in the Dolichoderinae subfamily, Hölldobler and Carlin (1985) found that the Australian meat ant *Iridomyrmex purpureus* is oligogynous, i.e., multiple queens share a nest but do not tolerate each other and relegate themselves to different areas of the nest. Further genetic analysis confirmed that oligogynous *I. purpureus* queens are unrelated and share a workforce (Carew et al., 1997). Oligogyny has also been documented in the subfamily Formicidae (*Camponotus ligniperdus,* Gadau et al., 1998; *Camponotus herculeanus*, Seppä and Gertsch, 1996).

ECOLOGICAL DRIVERS OF NON-KIN SOCIALITY

Group living may have its evolutionary origins across a particular set of ecological conditions that favor nest sharing and/or cooperation (Arnold and Owens, 1997; Krause and Ruxton, 2002; Rubenstein and Abbot, 2017). For non-kin groups especially, local ecology may be a prominent driver of group formation in the absence of strong indirect fitness benefits. Below, we discuss evidence for the evolution of non-kin sociality in the Hymenoptera as driven by five major ecological conditions/constraints: (1) predator and parasite pressures, (2) intraspecific competition, (3) physiological constraints, (4) productivity constraints, and (5) climatic stressors. Importantly, the distinctions we make between these five factors do not represent mutually exclusive conditions; rather, they are highly interactive and may even represent flip sides of the same environmental selective pressures (e.g., productivity constraints that arise from intense intraspecific competition). Together, these conditions may give rise to fitness differentials between solitary and social individuals when benefits of group living outweigh intrinsic costs of resource sharing.

Predator and Parasite Pressures

The need for communal defense represents one prominent benefit of nesting with non-kin. In particular, social defensive strategies often arise in contexts where brood is vulnerable to predation or parasitism (Alexander, 1974; Krause and Ruxton, 2002; Ward and Webster, 2016). Importantly, social nest defense can be a passive, emergent property of shared nesting rather than actively cooperative behavior. The presence of multiple females (or even males; Kukuk and Schwarz, 1988) in the nest can deter invaders by decreasing the daily time window in which the nest is unattended (Lin and Michener, 1972; Wcislo and Tierney, 2009). In other cases, labor may be divided such that guarding is a functional role of certain group members, often subordinates (Hogendoorn and Velthuis, 1995; Dunn and Richards, 2003). Indeed, task specialization on guarding can even emerge spontaneously among forced, unrelated associations of normally solitary individuals, suggesting that improved nest defense can arise in in communal nests from existing behavioral repertoires (Jeanson et al., 2005; Holbrook et al., 2009, 2013).

Although predator/parasite pressures have been broadly implicated in social evolutionary transitions (Michener and Lange, 1958; Lin and Michener, 1972; Krause and Ruxton, 2002; Wilson and Hölldobler, 2005), empirical demonstrations of the effectiveness of group defense in non-kin systems are sparse. For the sweat bee *Agapostemon virescens*, Abrams and Eickwort (1981) found that communal nests were more effectively defended against the cleptoparasite *Nomada articulata* than were solitary nests. Indeed, Lin and Michener (1972) consider parasite/predator pressures to be the major driver of sociality in the Halictidae (see also Michener and Lange, 1958). Similarly, co-founding wasps may experience reduced predation from birds and mammals relative to solitary foundresses, likely due to more continuous nest guarding (Strassman et al., 1988; Tindo et al., 2008). For other non-kin groups, guarding may function to repel conspecific intruders, but may not be an effective defense against predation and parasitism. For the facultatively social bees *Xylocopa virginica* and *Halictus ligatus*, rates of brood parasitism by Bombyliid flies were found to be no different between solitary and social nests, despite increased guard presence in social nests (Richards and Packer, 1998; Prager, 2014). Similarly, though multiple *Polistes* wasp foundresses may provide effective protection against intraspecific usurpation (Gamboa, 1978; Gamboa et al., 1978; Klahn, 1988), they may be no more effective in guarding against predators (Gamboa, 1978; Gamboa et al., 1978; Gibo, 1978) and parasites (Gamboa et al., 1978) than solitary foundresses, despite more continuous guard presence (Gamboa et al., 1978). However, co-founding may provide important benefits during recovery from predation attempts (Gibo, 1978; Strassman et al., 1988).

Intraspecific Competition and Resource Limitation

Grouping may arise as a response to limiting resources, especially nesting sites and food (Emlen, 1982; Hatchwell and Komdeur, 2000). Environments characterized by strong intraspecific competition may favor cooperative strategies that allow groups to exploit resources. In many cases grouping occurs in densely populated or saturated environments. Indeed, pleometrosis and primary polygyny in ants have been associated in several species with high population density (Tschinkel and Howard, 1983; Rissing and Pollock, 1986, 1991; Bennet, 1987; Trunzer et al., 1998). Likewise, for the facultatively polygynous harvester ant, *Pogonomyrmex californicus*, sites dominated by polygyny have higher colony density than primarily monogynous sites (Haney and Fewell, 2018). Further, colonies in the polygynous population have lower reproductive output than colonies from the monogynous population. Experimental food supplementation increased reproductive output of polygynous colonies to that of colonies from the monogynous population, suggesting that competitive, food-scarce conditions drive cooperation in this species (Haney and Fewell, 2018). Similarly, bees may adopt non-kin social strategies under food-scarce conditions, even in the absence of productivity benefits of group living. For the facultatively social carpenter bee *X. pubescens*, solitary nests typically outperform social nests in terms of reproductive output, due to brood mortality that results from dominance competitions in social nests (Hogendoorn, 1991, 1996). However, under conditions of food scarcity, social nesting can provide an important safeguard against pollen robbery, outweighing costs of nest sharing (Hogendoorn, 1991; Hogendoorn and Velthuis, 1993).

Nest sites can also be major limiting resources, favoring social strategies that enable nest sharing and/or increase the likelihood of nest inheritance. Carpenter bees are strongly limited by access to nest sites, creating intense competition for constructed nests that results in frequent supersedure and usurpation (Gerling et al., 1989; Buchmann and Minckley, 2019). Social nesting could feasibly provide an important defense against the threat of nest invasion, but empirical studies have demonstrated that guards of *X. pubescens*, though potentially valuable in preventing pollen robbery, do not effectively defend the nest from usurpers (Hogendoorn and Velthuis, 1993, 1995). Instead, subordinate joiners are likely hopeful reproductives that queue for reproductive opportunities upon the death of the dominant bee and subsequent nest inheritance (Hogendoorn and Velthuis, 1995; Richards and Course, 2015; Vickruck and Richards, 2018). Nest inheritance is likewise important for co-founding wasps (Reeve, 1991; Leadbeater et al., 2011), especially for species that reuse old nests (Queller and Strassmann, 1988). Similarly, for many communal bees, group living enables shared exploitation of valuable nest sites (Michener, 1974). In all these cases, intraspecific competition for nests promotes group living and interacts with other ecological constraints, especially energetic and labor constraints on nest construction.

Energetic and Physiological Constraints

Non-kin groups may also form in contexts that impose steep physiological costs on independent breeders. For example, animals that invest in energetically costly nest building behaviors may experience selection for strategies that reduce founding costs, such as cooperative building and/or nest inheritance (Hansell, 1987). Cooperative nest building has been documented broadly across Hymenopteran non-kin groups (West-Eberhard, 1969; Bartz and Hölldobler, 1982; Tschinkel and Howard, 1983; Rissing and Pollock, 1986; Peeters and Andersen, 1989; Danforth, 1991; Bernasconi and Strassmann, 1999; Hunt and Toth, 2017). In some cases, these benefits have been linked to ecological conditions and energetic constraints. The ground-nesting communal bee *Perdita portalis* excavates nests through a dense, clay layer of soil, prompting Danforth (1991) to propose energetic costs of nest construction as a major driver of sociality in this environment. Challenging excavation through hard soil may likewise favor cooperative nest construction strategies in the communal bee *Macrotera texana* (Danforth et al., 1996). Carpenter bees may also face particularly high energetic costs of nest building, due to the tendency of many *Xylocopa* species to nest in dense wood substrate. For the carpenter bee *X. sonorina*, the energetic cost of new nest construction is higher on average than the cost of nest inheritance, even accounting for the potential cost of renovating overused tunnels (Ostwald et al., 2021b). In this group, and more broadly, high costs of nest building can underlie intraspecific competition for existing nests. These costs may incentivize social strategies such as reproductive queuing or communal nesting, even at the expense of uncertain reproductive opportunities.

Beyond energetic costs, nest building behavior can impose physiological wear and damage. In arid habitats, nest construction behaviors could be constrained more by desiccation risk than by energetic costs. For many desert ants, nest excavation causes cuticular abrasion that increases water loss rates (Johnson, 2000), exacerbating desiccation risk, which is a major cause of foundress mortality (Johnson, 1998). Cooperative nest excavation during founding poses an important possible solution to this challenge. However, the physiological costs of excavation may not be shared equally among co-foundresses (Fewell and Page, 1999). Cahan and Fewell (2004) measured excavation task specialization in experimental pairs of the facultatively polygynous *Pogonomyrmex californicus*, with foundresses collected either from a typically group-founding or typically solitary-founding population. For both populations, more than half of foundress pairs divided excavation labor asymmetrically, with one foundress emerging as an excavation specialist. However, pairs from the group-founding population showed smaller asymmetries in excavation performance (Cahan and Fewell, 2004). These findings suggest that while some foundresses may experience disproportionate costs of excavation, cooperative strategies overall can reduce physiological costs of excavation for a significant portion of the population. Cooperative nest excavation and maintenance may likewise be important for some ground-nesting social bees (Danforth, 1991), but the extent to which nest excavation behavior is physiologically constrained in these groups is still unclear.

Productivity Constraints

Cooperation among non-kin can also improve productivity under harsh or competitive conditions. In particular, cooperative founding may provide competitive advantages in conditions that favor rapid nest establishment via worker production. Group founding in ants has been associated both with faster initial worker production and accelerated colony growth (Tschinkel and Howard, 1983; Rissing and Pollock, 1987; Deslippe and Savolainen, 1995; Eriksson et al., 2019; Ostwald et al., 2021c). Rapid production of a large workforce may beneficially accelerate incipient groups through the vulnerable founding period, providing a critical survival advantage for cooperatively founded colonies (Clark and Fewell, 2013; Ostwald et al., 2021c). These advantages may be especially important for colonies vulnerable to intraspecific brood raiding. Cooperative founding has been shown to improve colony survival and success during brood raiding, likely due to the protective effect of larger colony sizes (Bartz and Hölldobler, 1982; Rissing and Pollock, 1987, 1991; Eriksson et al., 2019). Increased colony size in multi-foundress nests is also associated with reduced colony failure rates for the paper wasp *Polistes dominula* (Tibbetts and Reeve, 2003). Importantly, cooperative foundresses may experience enhanced colony growth without increasing costly individual investment in sterile worker production. Multi-queen colonies of the harvester ant *P. californicus* experience faster colony growth than single queen colonies, but lower per-queen worker production (Ostwald et al., 2021c). The ability to assemble a large workforce while minimizing individual investment in non-reproductive offspring may represent an important physiological benefit of cooperation with non-relatives.

Specifically, individuals may face productivity constraints associated with resource exploitation. For example, the communal bee *Macrotera texana* faces severe reproductive time constraints due to its foraging dependence on *Opuntia* flowers that bloom for only 2–3 weeks per year (Danforth et al., 1996). Cooperative nest excavation likely enables females to exploit this time-limited resource by accelerating nest founding (Danforth et al., 1996). Similarly, increased colony activity levels in polygynous *P. californicus* colonies suggests both increased worker production and corresponding enhanced efforts to capitalize upon limiting food resources (Haney and Fewell, 2018). In this way, productivity constraints interact strongly with resource limitation and intraspecific competition.

Importantly, worker production benefits may not translate to enhanced production of reproductives. For *P. californicus* as well as for the sweat bee, *Halictus ligatus*, group-founding nests produce more workers but fewer reproductive offspring than solitary-foundress nests (Richards and Packer, 1998; Haney and Fewell, 2018). *Polistes* foundress associations are likewise associated with reduced per-capita reproductive output (Queller and Strassmann, 1988; Reeve, 1991), despite increased worker production in some species (Tibbetts and Reeve, 2003). These cases suggest that cooperation often functions not as a means to enhance reproductive output under ideal conditions, but rather as a strategy to minimize losses under constraining or challenging environmental conditions.

Climatic Stressors

Climatic factors represent fundamental ecological drivers of group living across animal taxa. In particular, cooperation may be favored in harsh or stochastic climates (Arnold and Owens, 1997; Jetz and Rubenstein, 2011; Rubenstein, 2011; Griesser et al., 2017; Lukas and Clutton-Brock, 2017; Kennedy et al., 2018). In insects, climate likewise mediates the expression of social behavior, especially through impacts on development time and seasonal activity windows, which affect the available time for rearing workers and therefore the potential for colony life to emerge (Eickwort et al., 1996; Hunt and Amdam, 2005; Hirata and Higashi, 2008; Fucini et al., 2009). These factors may be important in the evolution of eusociality by promoting generation overlap in the nest. For non-kin groups, however, that arise from stable cooperative relationships between unrelated individuals, the effects of climate on group formation are relatively unexplored.

Nevertheless, several studies point to prominent roles for climatic conditions, especially environmental temperatures, in facilitating non-kin cooperation. Among *Polistes* paper wasps, which can found nests with non-relatives, cooperative nest founding is associated with high temperature variability, perhaps due to buffering cooperation of sociality in unpredictable environments (Sheehan et al., 2015). Polygyny in ants has also been associated with harsh thermal environments (Heinze, 1993; Heinze and Hölldobler, 1994; Heinze and Rüppel, 2014) and with success of invasive species in their introduced environments (Holway et al., 2002; Tsutsui and Suarez, 2003). Future work should clarify mechanisms underlying this link between cooperation and success in harsh, variable, or novel thermal environments.

Precipitation can also influence the relative costs and benefits of grouping. Arid environments and drought conditions can increase soil hardness, potentially increasing excavation costs and exacerbating nest limitation for ground nesting bees, ants, and wasps (Wcislo, 1997; Michener, 2007; Purcell, 2011). Under drought conditions, Bohart and Youssef (1976) found that 30% of nests of the normally solitary sweat bee *Lasioglossum galpinsiae* were provisioned by multiple females. In desert ants, group founding may be a by-product of the tendency to seek refuge from desiccating conditions in shared belowground spaces (Pfennig, 1995). Under desiccating conditions, group-founding by the desert seed-harvester ant *Veromessor pergandei* enhanced queen survival and water content relative to solitary queens, though the mechanism for this advantage is unclear (Johnson, 2021). Shared foraging duties could feasibly reduce risk of desiccation in desert habitats. Cahan and Fewell (2004) suggest that a group-founding population of the harvester ant *P. californicus* occupies a habitat with lower and less predictable summer precipitation than sites occupied by solitary founding populations, suggesting possible desiccation constraints. In less arid habitats, extended periods of rain can cause nest failure for ground-nesting species. For the sweat bee *Halictus ligatus*, foundress cooperation may provide protection against rain-induced nest failure through enhanced nest maintenance (Richards and Packer, 1998). As such, like environmental temperature, precipitation can alternately promote or constrain cooperative behavior among non-relatives.

DISCUSSION

Sociality can be understood as an adaptive response to ecological conditions. Non-kin groups present valuable test cases for hypotheses about the ecological drivers of group formation, in particular, because communal and co-founding strategies are nearly always facultative at the individual or population level (Ross and Matthews, 1991; Michener, 2007; Heinze et al., 2017).

Studying non-kin groups usefully controls for indirect fitness benefits, thus enhancing our understanding of other, relatively neglected drivers of group formation. These systems have yielded important intraspecific demonstrations of the role of ecology in determining the adaptive value of grouping behavior. Here, we have explored five central ecological factors expected to interact with the expression of social behavior: interspecific pressures from predators and parasites, intraspecific pressures over limited resources, environmental constraints on individual physiology and productivity, and stressors associated with climate. Evidence from across Hymenopteran systems indicates that these conditions play a pivotal role in shaping non-kin social strategies.

Importantly, these ecological drivers of sociality are highly interactive. Efforts to understand sociality across a single environmental axis are limiting and often yield contradictory results (e.g., sociality alternately increasing and decreasing with latitude; Purcell, 2011). Instead, integrative approaches that accommodate these interactions can provide important insights into the complex conditions underlying grouping responses. Studies in Hymenopteran systems have emphasized interactions among intraspecific, interspecific, and abiotic selective pressures. For example, sociality can be a response to intraspecific competition for access to nests (Gerling et al., 1989; Leadbeater et al., 2011). This competition is often a direct product of physiological constraints associated with nest construction behavior (Johnson, 2000; Ostwald et al., 2021b), which can be exacerbated by climatic stressors such as low precipitation (Wcislo, 1997; Purcell, 2011). This particular nexus of challenges is an important driver of group formation among the communal and parasocial bees and polygynous ants (Danforth, 1991; Danforth et al., 1996; Cahan and Fewell, 2004). Highly competitive environments can also give rise to cooperative strategies that mitigate worker production constraints experienced by solitary foundresses. Accelerated worker production is a major benefit of cooperation among ant foundresses vulnerable to brood raiding in contexts dominated by intraspecific competition (Bartz and Hölldobler, 1982; Rissing and Pollock, 1987, 1991; Eriksson et al., 2019). Productivity constraints may also be important drivers of grouping in environments dominated by predation pressures; for group-founding wasps, increased colony sizes can provide essential resilience following predation attempts (Strassman et al., 1988). Together, these examples suggest shared sets of ecological conditions that favor cooperative behavior even when relatedness is low or absent among group members. Importantly, these conditions are not restricted geographically but instead occur at intersections of particular selective pressures that can occur across a wide variety of habitat types.

These findings in non-kin groups of ants, bees, and wasps parallel known drivers of social evolution in non-insect social systems, both kin and non-kin. Ecological constraints are prominent, known drivers of cooperative breeding in birds and mammals (Emlen, 1982, 1984; Arnold and Owens, 1997; Hatchwell and Komdeur, 2000; Shen et al., 2017). Inheritance tactics in nest-limiting environments may favor delayed dispersal and nest joining (Woolfenden and Fitzpatrick, 1978; Emlen, 1984). As with the ground-nesting ants and bees, nesting constraints may be physiological, and can be exacerbated by climatic conditions: nest excavation costs in arid conditions have been proposed as a major driver of sociality in the African mole-rats (Jarvis et al., 1994; Faulkes et al., 1997; Hansell, 2005). More broadly, low and unpredictable rainfall has been associated with the global biogeography of cooperatively breeding mammals (Lukas and Clutton-Brock, 2017). Environmental stochasticity has also been implicated in the global distribution of cooperative breeding in birds (Jetz and Rubenstein, 2011), suggesting important links between cooperation and environmental uncertainty that parallel trends described in *Polistes* foundress associations (Sheehan et al., 2015).

Strengthening the conceptual links among Hymenopteran and vertebrate sociality has great potential for the development of broader evolutionary frameworks explaining non-kin cooperation. Vertebrate research has benefited from a more comprehensive understanding of the taxonomic distribution of kin and non-kin sociality, especially among the cooperatively breeding birds. This knowledge base has enabled valuable phylogenetic studies highlighting the roles of environmental and life history factors in shaping social organization (Riehl, 2013; Downing et al., 2015, 2020; Cornwallis et al., 2017). The social Hymenoptera likewise present special opportunities to study non-kin sociality because it occurs frequently across closely related lineages. To our knowledge, this comparative approach has not yet been applied to the Hymenoptera in the context of kin vs. non-kin social evolution, but may be feasible for those taxa in which non-kin sociality is better documented, especially the polygynous ants.

Beyond this comparative framework, the literature on vertebrate social systems can provide social insect researchers with valuable approaches for studying direct benefits of cooperation. The social vertebrate literature is rich in explorations of the costs and benefits of well-defined cooperative behaviors, from hunting and defending food (Packer and Ruttan, 1988; Lucas and Brodeur, 2001) to detecting and repelling predators (Hamilton, 1971; Foster and Treherne, 1981) or successfully rearing offspring (Ebensperger et al., 2007; Hodge et al., 2009). Likewise, studies should investigate direct benefits of cooperative behaviors in Hymenopteran societies, for example, the effectiveness of nest defense in social vs. solitary bee nests (as in Hogendoorn and Velthuis, 1993; Prager, 2014), or the consequences of shared foraging duties in ant and wasp foundress associations (Cahan and Fewell, 2004). Importantly, the exchange of theories and ideas between vertebrate and invertebrate sociality research should be bi-directional. Insights from Hymenopteran systems have the potential to overcome many of the limitations of work with vertebrate systems. Especially given their short generation times and experimental tractability in lab settings, insect systems have the potential to fill gaps in our broader understanding of the long-term direct fitness outcomes of cooperation over multiple generations.

Current understanding of social evolution among unrelated individuals is constrained by limited knowledge of the full diversity of Hymenopteran taxa that form non-kin groups. The incidence of non-kin cooperation is likely to be greatly underestimated due to the tendency of non-kin groups to occur within otherwise solitary populations (Ross and Matthews, 1991; Michener, 2007; Heinze et al., 2017), and due to limitations associated with quantifying relatedness in some species. This knowledge gap can be addressed with simple behavioral techniques (e.g., mark-recapture or observations of nest joining; Abrams and Eickwort, 1981; Peso and Richards, 2011) and inexpensive genotyping methods (e.g., microsatellites; Moore and Kukuk, 2002). Other techniques, like radio-frequency tracking (Sumner et al., 2007; Kissling et al., 2014), have the potential to reveal nest switching patterns that maintain low relatedness in some insect groups. A first priority in future research on non-kin sociality should be to expand our understanding of the diversity of non-kin systems via integrated behavioral and molecular research. Many of the species highlighted in **Table 1** currently possess incomplete evidence for non-kin sociality, especially among the wasps and bees. It is likely that non-kin groups form among many other, related species for which kinship has not yet been quantified. The same may be true for similarly structured social groups outside the Hymenoptera, especially among the termites, which can form polygynous colonies through colony fusion (DeHeer and Vargo, 2004, Deheer and Vargo, 2008; Korb and Roux, 2012).

Beyond characterizing the organization and formation of these groups, studies that relate social founding strategies to ecological conditions or compare social and solitary strategies in sympatry represent promising directions for future research. Particularly illuminating would be controlled experimental studies relating social condition to ecological conditions and, especially, to fitness outcomes. The abundance of facultatively social non-kin groups provides diverse, experimentally tractable systems in which social condition can be observed and even manipulated within a single species, thus avoiding the pitfalls of comparisons across species with very different evolutionary histories. Manipulative studies such as these could rigorously test hypotheses about proposed drivers of sociality, providing insights into the ecological conditions at the origins of group living.

CONCLUSION

The ecological drivers of non-kin cooperation represent a highly overlapping suite of conditions that interact to constrain solitary reproductive opportunities. Integrative research that accommodates these interactions has the potential to reveal common principles underlying social evolution broadly across animal taxa and across kin and non-kin groups. Our current understanding of the full diversity of non-kin sociality in the Hymenoptera is highly limited, but existing analyses suggest that groups containing non-relatives are more widespread than previously acknowledged. Future work should quantify relatedness across a diversity of species, and leverage these systems as models for evaluating the ecological conditions that favor group formation. Studies of known non-kin groups in the Hymenoptera have emphasized the role of harsh, competitive environments in selecting for cooperative strategies even in the absence of indirect fitness benefits. These findings parallel patterns more broadly across animal groups that indicate a major role for ecological constraints in shaping diverse forms of sociality.

AUTHOR CONTRIBUTIONS

MO wrote the main manuscript. BH wrote the section on ant sociality. All authors contributed to manuscript editing and developing the concept for the review.

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