



Collective personalities: present knowledge and new frontiers

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Abstract

Collective personalities refer to temporally consistent behavioral differences between distinct social groups. This phenomenon is a ubiquitous and key feature of social groups in nature, as virtually every study conducted to date has documented repeatable between-group differences in collective behavior, and has revealed ongoing selection on these traits in both the laboratory and field environments. Five years ago, foundational reviews by Bengtson and Jandt pioneered this topic and delimited the present knowledge on collective personality. Here, we update these reviews by summarizing the recent works conducted in the field's most prominent model systems: social spiders and eusocial insects. After presenting how these recent works helped scientists to better understand the determinants of collective personality, we used a trait-by-trait format to compare and contrast the results and thematic trends obtained in these taxa on 10 major aspects of collective personality: division of labor, foraging, exploration, boldness, defensive behavior, aggressiveness, decision-making, cognition, learning, and nest construction. We then discuss why similarities and dissimilarities in these results open the door to applying numerous theories developed in evolutionary behavioral ecology for individual traits (e.g., life history theory, game theory, optimal foraging theory) at the colony level, and close by providing examples of unexamined questions in this field that are ripe for new inquiries. We conclude that collective personality, as a framework, has the potential to improve our general understanding of how selection acts on intraspecific variation in collective phenotypes that are of key importance across arthropod societies and beyond.

Keywords Personality · Behavior · Sociality · Arachnids · Insects · Collective behavior · Eusocial

Introduction

If you have ever had the misfortune of being swarmed by bees or wasps, or have witnessed ants or termites angrily emerge from underground tunnels in response to your disturbance, then you have observed a type of collective behavior. If you repeatedly antagonize many colonies, you might notice that colonies often differ consistently in how they respond to your meddling. That is, different colonies exhibit distinct “personalities.” While societal traits like aggressiveness may be the most readily observable and conspicuous, there are many other ways that colonies can differ behaviorally that is

relevant to their functioning and survival. Individual societies may for instance differ in how broadly they explore and forage, how well they attend to their young, how strictly they divide their labor among tasks, or how they build or excavate complex 3-dimensional nest structures, and so on.

Here, we survey the most recent research on *collective personality* in social arthropods and provide a roadmap of promising paths this field could take. A few years ago, Jandt et al. (2013) and Bengtson and Jandt (2014) produced exhaustive reviews of the literature on this topic, which have since inspired more than 100 descendant papers. Although model taxa for these investigations have included some vertebrates

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(e.g., birds, fish), the majority of studies have used social arthropods for their investigations. Here, we aim to comment on the field's exponential progress since the last reviews, and compare and contrast the findings gleaned from the field's most prominent model systems: social spiders and eusocial insects. After presenting how these recent works improved our understanding of the determinants of collective personality, we use a trait-by-trait format to compare and contrast the results and thematic trends obtained in these species on 10 major aspects of collective personality: division of labor, foraging, exploration, boldness, defensive behavior, aggressiveness, decision-making, cognition, learning, and nest construction. We end by offering a variety of new hypotheses regarding how collective personality may interact with other fields of behavior and ecology, including colony life history and performance, and population and community ecology.

The determinants of collective personality

What is collective personality?

Personality is a property of a population or group, and is usually defined as the presence of temporally consistent behavioral differences between individuals (Sih et al. 2004, 2012). The aggregate is said to have personality, while each individual comprising the aggregate falls somewhere on a spectrum with respect to a particular behavioral trait. Often, individuals are said to possess a particular "behavioral type" or BT, or sometimes "personality type" (e.g., docile vs. aggressive individuals) when the distribution is less continuous and more categorical/bimodal. Furthermore, the term "individual" can apply both to individual organisms as well as cohesive social groups (Jandt et al. 2013). This is particularly relevant in eusocial species, where colonies can be viewed as extended phenotypes of the queen, and the queen + workers as a type of "superorganism" (Hölldobler and Wilson 2009). Yet, the concept of inter-group differences in collective behavior can apply to other social groups as well. Thus, "collective personality" refers to *the presence of temporally consistent behavioral differences exhibited between distinct social groups* (Jandt et al. 2013; Bengston and Jandt 2014; Jandt and Gordon 2016).

How does collective personality arise?

While it may be sufficient in many instances to simply note that behavioral variation exists among groups, and measure its ecological effects, understanding the mechanisms giving rise to between-group personality is necessary to make predictions about the flexibility and heritability of group traits, and how they might respond to selection. For instance, collective behaviors are a product of both environmental and genetic factors, and knowing the relative contribution of these on collective behavior is

central to understanding the evolution of collective personality, as well as determining how researchers frame their findings and design future experiments. Explanations for the origins of collective personality fall into three, non-mutually exclusive categories of influence: genetics, physiology, and environment.

Genetics Variation in the genetic composition of a group, as well as in gene expression within group members, can be important determinants of collective personality. The queens of eusocial insects can be inseminated by one or multiple males (Strassmann 2001; Kronauer et al. 2004), and mate number varies widely both within and among species (Cole 1983; Strassmann 2001). The more males a queen mates with, the more genetically diverse her workers will be, which is expected to result in the expression of a variety of behavioral temperaments in workers. This is supported, for instance, in honeybees, where genetic variation explains worker learning ability (Chandra et al. 2000), foraging propensity and preference (Page and Robinson 1991; Page et al. 1998), and defensive behavior (Breed et al. 2004), as well as division of labor (Robinson 1989; Page and Robinson 1991; Page et al. 1998). However, species whose queens mate only once still give rise to behaviorally diverse societies (Dornhaus et al. 2008; Jandt and Dornhaus 2009; Jandt et al. 2009), indicating that genetic variation both within and between queens contribute to the emergence of individual- and colony-level personality. Interestingly, individual and collective personality variation can also arise in genetically curbed social taxa, such as social spiders (Pruitt and Riechert 2011a; Holbrook et al. 2014; Wright et al. 2014, 2015). There, collective personality can arise due to differences in gene expression between colony members (Ben-Shahar et al. 2002; Ingram et al. 2005; Zayed and Robinson 2012; Rittschof 2017), which is influenced by a multitude of factors such as individual or colony experience (Niemela et al. 2012; Rittschof 2017), nutrition (Toth and Robinson 2005; Wheeler et al. 2006; Ament et al. 2008; Ament et al. 2010), social environment (Huang and Robinson 1996; Beshers et al. 2001), or age (Sullivan et al. 2000; Beshers et al. 2001; Robinson and Ben-Shahar 2002). Discrete colony-level social polymorphisms in behavior can also be under strong genetic control, such as in the fire ant *Solenopsis invicta*, where worker tolerance of polygyny as well as nest initiation behavior rests on a single locus polymorphism (Keller and Ross 1998; Ross and Keller 2002; Wang et al. 2013). Although variation in collective personality emerges even in the absence of strong genetic determination (discussed below), genetic underpinnings are usually *required* for there to be an effective response to selection on collective traits. Notably, the transmission of colony-level phenotypes down lineages has rarely been demonstrated (Pruitt and Goodnight 2014; Pruitt et al. 2017a), even circumstantially (Gordon 2013).

Physiology As individuals age, many physiological changes occur that lead to changes in their behavior and thus likely

affect the personality of their group. In honeybees and most eusocial insects, colonies organize work via age-related division of labor known as temporal polyethism (Seeley 1982). New workers tend to remain inside the colony as nurses, and take on more complex and risky foraging duties outside the colony as they age. Because changes in the patterns of brain gene expression co-occur during this transition (Whitfield et al. 2003), variation in age demographics between colonies can contribute to the expression of distinct colony-level phenotypes. In some insect societies, however, such as the ant *Pheidole dentata*, worker age does not determine which tasks are performed, but rather determine how *expansive* an individual's behavioral repertoire becomes (Seid and Traniello 2006). This phenomenon is known as repertoire expansion.

Additionally, many behavioral differences in eusocial insects arise due to individuals producing different levels of hormones. For example, juvenile hormone (JH) has been linked with aggressiveness (Pearce et al. 2001; Tibbetts and Huang 2010), dominance behavior (Barth et al. 1975; Tibbetts and Huang 2010), behavioral development (Fahrbach and Robinson 1996; Sullivan et al. 2000), division of labor (Schulz et al. 2002), and reproductive behavior (Barth et al. 1975; Riddiford 2012). Other factors that can influence physiology and, subsequently, behavior, include diet, nutrition, and fat content (corpulence) (Blanchard et al. 2000). These state-dependent behaviors of individuals can also influence group behavior, such as when group foraging patterns are influenced by the hunger or nutritional state of individuals (Krause et al. 1992; Krause 1993), and variation in any of the abovementioned physiological traits can conceivably shape the way a colony will behave.

Environment Collective behaviors are often determined by external (i.e., environmental) factors rather than internal (i.e., genetic and physiological) factors (Bengston and Jandt 2014), which can be biotic or abiotic in nature. For instance, the location of a colony can determine how much light it receives, and the internal temperature, humidity, maximum size, and geometry of nest architecture. Many of these elements have been shown to directly influence colony-level behavior (Traniello et al. 1984; Gordon 1996; Gordon et al. 2011, 2013; Wray and Seeley 2011; Dornhaus et al. 2012; Pinter-Wollman et al. 2012; Modlmeier et al. 2014a; Pinter-Wollman 2015; Segev et al. 2017). Additionally, weather (Pinter-Wollman et al. 2012), resource abundance (Downs and Ratnieks 2000; Bengston et al. 2014; Pruitt and Goodnight 2014), and environmental variation across their range can also influence the collective behavior of groups (Pankiw 2003; Bengston and Dornhaus 2014; Bengston et al. 2014; Segev et al. 2017). Biotic factors, such as social environment, the presence or absence of predators, distance to neighboring colonies, the presence of “keystone” individuals and adults or queens, or previous group experience can also shape functional differences in group behavior (Suryanarayanan and Jeanne 2008; Pamminger et al. 2011; Suryanarayanan et al. 2011; Kleeberg et al. 2014;

Laskowski and Pruitt 2014; Modlmeier et al. 2014d; Pruitt and Keiser 2014; Modlmeier et al. 2015; Wright et al. 2016a, 2017; Norman et al. 2017; Keiser et al. 2018).

How is within-colony and between-colony variation in collective personality maintained?

One perennial question is how functional variation in individual or collective behavior is maintained. After all, if there are fitness costs and benefits associated with behaving a certain way, we might expect selection to act as a homogenizing force on within-colony behavioral variation and among-colony differences in collective personality. However, the ubiquity of personalities within animal societies and across groups suggests this notion is false. Here, we discuss four processes that could explain how variation in collective personality is maintained both within and between colonies.

Frequency-dependent selection The hawk/dove model is a classic model in the game theory that describes how the costs and benefits associated with one behavioral strategy can be inversely related to an alternate strategy in a population (Smith 1979). Thus, the costs and benefits of a behavior can be frequency-dependent and result in fluctuations in the genetic and behavioral makeup of a population (Nonacs and Kapheim 2007, 2008). The same can occur within social groups, where different behavioral types enjoy a selective advantage relative to others, until a point is reached where the pendulum of selection begins to swing the other way. This type of selection prevents any one individual-level behavioral type from becoming universal, and thus promotes within-group behavioral diversity. We propose that these classic trade-off models developed in the context of solitary species could play a role in maintaining between-group variation in collective personality as well, via frequency or density-dependent selection on colony behavior. For instance, aggressive colonies may be favored in populations of strictly docile colonies, but suffer unreasonable costs that drive their performance beneath that of docile colonies when aggressive societies become common. The costs of aggressive-aggressive conflict at the colony level, a la the hawk-dove game, are plausibly quite high and could be fairly estimated.

Social heterosis An individual's behavior cannot be two things at the same time; they cannot be simultaneously bold and shy, or aggressive and docile. Unlike a single individual, a group can harbor as many genetic and behavioral variants as there are individuals, which allows for any mutual benefits of this diversity to be shared by all group members, and even the group as a single unit. The benefit of within-group behavioral diversity is commonly referred to as “social heterosis.” In the social spider *Anelosimus studiosus*, for instance, different colony compositions are selected in different habitats based on resource abundance (Pruitt and Goodnight 2014), and colonies of mixed compositions outperform

monotypic compositions (Pruitt 2013). Just like individuals within a colony, we propose that group performance may be contingent on the phenotypic neighborhood in which colonies reside, and that the classic theory on social heterosis at the individual level could be applied to the level of the group. For example, one might propose that colonies surrounded by neighbors of unlike behavioral tendencies may compete less for prey resources, may occupy different kinds of nests, or may subtly partition their activities temporally in a manner that reduces conflict. We even propose that neighboring colonies may, over time, begin to behave more dissimilarly to enjoy such benefits—a la character displacement but at the level of collective traits.

Behavioral reaction norms Individuals vary in their average behavior across contexts and in their behavioral plasticity. Previously, these two aspects of an individual—personality and plasticity—had been treated as separate entities. However, these two factors are now seen as tightly intermingled. A behavioral reaction norm approach describes how an animal varies in a certain behavior, say aggressiveness, over some environmental gradient, such as temperature, population density, or predation risk (Dingemanse et al. 2010). The degree of plasticity exhibited in contrasting environments is largely due to the relative contribution of either genetics or environment to an observed behavior. Variation in individuals' behavioral reaction norms can beget contrasting levels of within-population variation in individual-level personality across environments, and can be linked with individual performance. At the colony level, it is almost certainly true that entire societies will likewise vary in their collective behavioral reaction norms. In groups, however, the magnitude of behavioral reaction norms exhibited may vary based on the relative contribution of genetics and environment to an observed behavior or, alternatively, the amount of behavioral variation within a colony. The ability to experimentally manipulate colony compositions in a split colony design makes many social species well-suited to address such questions. However, the magnitude of these differences and their functional consequences remain unknown.

Temporal trade-offs Behaviors that promote success in one situation are often suboptimal in different circumstances. When this occurs, natural selection can pull in opposite directions depending on the time of year, the situation, or life stage of the organism, and this can help maintain variation in behavior (Wolf et al. 2007), or modify the behavioral composition over time as group size increases, decreases, or remains static while members die and are replaced. We propose that trade-off theory developed in the context of maintaining within-population variation due to conflicting selection pressures across situations could play an important role in the maintenance of collective personality and genetic variation between groups as well (e.g., (Lichtenstein et al. 2015; Pruitt et al. 2017b)). Whether trade-offs associated with collective

behavioral types are common is mostly unknown, but the possibility is difficult to ignore.

Insights from eusocial insect and arachnid societies

Eusocial insects are perhaps the most well studied of all animal societies, owing to their diversity, abundance, widespread distribution, and, most importantly, the high degrees of social complexity exhibited by these taxa. While we do not discount the importance and insight that could be gleaned from a thorough comparison of the collective personalities of eusocial insects alone, we have here chosen to compare them specifically to social arachnids, which are cooperative breeders. This was not an arbitrary decision. Behind eusocial insects, most research on collective personalities have been performed in social arachnids due to their local abundances, variation in degrees of sociality, and because sociality in arachnids has evolved independently numerous times (Agnarsson et al. 2006). Additionally, social spiders are easily manipulated in both the lab and field, and are similar in size to many eusocial insects in both brain and body. Therefore, a comparison between eusocial insects and social arachnids allows for a more comprehensive comparison than with many other groups. Over the last several decades, important progresses have been achieved in our understanding of 10 aspects of collective personality that are division of labor, foraging, exploration, boldness, defensive behavior, aggressiveness, decision-making, cognition, learning, and nest construction. Interestingly, much of this understanding comes from studies on eusocial insects and social spiders. In the following sections, we will use a comprehensive survey of the recent literature on these 10 aspects of collective personality in eusocial insects and social spiders, to present the current state of knowledge surrounding these forms of collective personalities and to discuss their similarities and their differences, as well as to call attention to major remaining gaps in our knowledge

Division of labor

Perhaps the most well-studied influence of individual-level personality on collective outcomes is personality-linked division of labor. Division of labor (DOL) describes a process where different individuals specialize in different tasks, thus presumably increasing overall group productivity and efficiency. For eusocial insects, this phenomenon is often studied in the context of caste ratios or continuous morphological variation among workers (Holldobler and Wilson 1990). Age-related DOL such as temporal polyethism or repertoire expansion has also been given its due attention (Seeley 1982; Seid and Traniello 2006). In other cases, differences in colony DOL seem to emerge without intrinsic differences among workers—for instance via self-reinforcement (Theraulaz et al. 1998b), age demography (Seeley 1982; Robinson et al.

1994), social dominance (Vanhonk and Hogeweg 1981), location in the colony or “foraging for work” (FEW) (Franks and Tofts 1994), social inhibition (Huang and Robinson 1992, 1996), or social network-based mechanisms (Gordon 1986, 1989; Pasquaretta and Jeanson 2018). Recently, however, DOL in association with individuals’ personality types, rather than their morphology or age, has captured the attention of behavioral ecologists. This trend is notable because most eusocial insect species lack discrete morphological castes beyond reproductives and workers. In the absence of distinct morphological differences, personality variation provides another cryptic axis of functional diversity that can help predict who will tend to perform which tasks, as well as their aptitudes for those tasks, and their propensity to switch tasks. We argue that DOL can and should be considered a collective personality trait, since different groups can exhibit temporally stable differences in their degree of division of labor due to differences in response thresholds (Robinson 1992), individual-level personality ratios (Holbrook et al. 2014; Wright et al. 2014), and potentially their nest structure.

Eusocial insects

For many insect societies, collective personalities are argued to be the result of individual variation in fixed response thresholds that shape which individuals tend to perform which tasks inside of a society. In honeybees, for instance, variation in sucrose responsiveness between individuals dictates colony-level nectar foraging behavior (Pankiw and Page 1999, 2003; Pankiw et al. 2001). Similar individual response thresholds, but for pheromones produced by larvae, influence recruitment to pollen (protein) foraging (Pankiw et al. 1998). Interestingly, individuals can vary in their response thresholds to a number of phenomena, such as task-related social interactions with larvae and other workers (Gordon 1996), so that individual differences in how workers respond to these interactions can produce marked differences in the collective behavioral tendencies of whole colonies. In contrast to classical studies on individuals’ fixed response thresholds, which are a sensory-based approach, studies on animal personality tend to focus on individuals’ latency to participate in one task or the frequency with which they engage in it (Wright et al. 2014). We propose that individuals’ performance in personality assays could be functionally linked to their response thresholds or the responsiveness of individuals’ thresholds to experience. If true, this would provide a link between individual-level personality and sensory biases, and help to mechanistically explain the large number of studies linking the personality composition of groups with division of labor. In eusocial insects, it should be noted that DOL has not yet been shown to correlate with variation among colonies in within-colony personality diversity per se (Dornhaus 2008). However, several studies have documented relationships between within-colony genetic diversity and colony success (Mattila and Seeley 2007), and this relationship is often argued to be mediated

through genotypic differences in behavioral tendencies (e.g., sucrose response) (Pankiw and Page 2000; Smith et al. 2008), which are a kind of personality variation.

Given that most eusocial insect societies, especially honeybees, organize labor by age, it is likely that inter-colony personality variation could be heavily influenced by the relative age distribution of workers between colonies, and that fluctuations in birth and death rates over time could result in fluctuations in colony-level personality. Similarly, species that exhibit age-related repertoire expansion, as opposed to temporal polyethism, may exhibit more stable collective personalities over time, given the increased behavioral plasticity of their older workers.

Social arachnids

In arachnids, studies of personality-based DOL have been conducted in three genera: tangle web spiders in the genus *Anelosimus*, arid-dwelling spiders from the genus *Stegodyphus*, and the New Guinean social spider *Achaeearanea wau* (Lubin 1995). In *An. studiosus*, individuals within a colony exhibit one of two behavioral types, docile or aggressive (Pruitt et al. 2008), and this distinction predicts individuals’ participation and proficiency at various tasks (Holbrook et al. 2014; Wright et al. 2014). Docile individuals assume brood care duties, while aggressive spiders engage in colony defense (Wright et al. 2014). The degree of DOL in this species is high (Holbrook et al. 2014), on par with those of many eusocial insects, such as bumblebees (Jandt and Dornhaus 2009) and harvester ants (Jeanson and Fewell 2008; Holbrook et al. 2011). In the field, colonies composed of only docile individuals grow quickly but die off in fewer generations because of invasion by predatory social parasites. Conversely, aggressive colonies do not so easily accumulate social parasites, but their deficient brood care practices prevent them from growing or proliferating as quickly as their docile counterparts. Colonies containing both docile and aggressive individuals enjoy the highest overall success (Pruitt and Riechert 2011b; Pruitt and Riechert 2011a; Pruitt 2012, 2013; Pruitt et al. 2012a). A closely related species, *Anelosimus eximius*, also exhibits DOL, but this is primarily related to age (Settepani et al. 2013), body size, and body condition (Ebert 1998) rather than personality. Three other social *Anelosimus* species—*A. rupununi*, *A. guacamayos*, and *A. oritoyaku*—experience higher foraging success when colonies are composed of a mixture of docile and aggressive spiders, suggesting that these species may also exhibit some degree of DOL during foraging (Pruitt et al. 2012b). Recent work suggests that behavioral compositions could be locally adapted in one species of *Anelosimus* and that this species may have evolved mechanisms of maintaining these optimal compositions if perturbed (Pruitt and Goodnight 2014; Pruitt et al. 2017a), possibly due to adaptive DOL.

African desert social spiders from the genus *Stegodyphus* build a three-dimensional communal nest and construct numerous two-dimensional capture webs that radiate away from it.

Several *Stegodyphus* species exhibit between-individual variation in boldness that has been linked to colonies' DOL and collective behavioral type. For instance, participation in prey capture is positively related to individuals' boldness and negatively associated with body condition in *S. dunicola* (Keiser et al. 2014; Wright et al. 2015, 2017). *S. dunicola* also exhibits DOL in defensive behavior, where bolder individuals are more likely to engage in defensive silk-spinning when attacked by predatory ants (Wright et al. 2016a) whereas shy individuals tend to adopt follower roles in risky tasks (Pruitt et al. 2017b). Trait diversity linked with DOL also increases over time as individuals become familiarized with nest mates and, conversely, sudden changes in group membership decreases group success in collective tasks and reduces DOL (Laskowski et al. 2016). In *S. sarisanorum*, boldness and condition are similarly related to task participation in prey capture (Grinsted et al. 2013; Settepani et al. 2013; Beleyur et al. 2015). In *S. mimosarum*, DOL in prey capture has been linked to body size (Wickler and Seibt 1993). Thus, across all three independently evolved social species of *Stegodyphus*, similar patterns of personality-based DOL emerge and appear to play a role in colony success.

Division of labor, whether personality-based or otherwise, has been observed in some subsocial spiders and other social arachnids. In the subsocial spider, *Amaurobius ferox*, there is some evidence for foraging DOL, since it has been observed that only a small, but consistent, subset of individuals initially attack prey, while most colony members never participate in subduing prey (Kim et al. 2005). In another subsocial species, *Australomisidia ergandros*, it was found that feeding-type compositions shifted in favor of scroungers over producers as group sizes increased (Dumke et al. 2016). Finally, in the cooperative pseudoscorpion *Paratemnoides nidificator*, which also exhibits DOL, the tasks that individuals perform are related to their age and sex, but personality has not been considered (Tizo-Pedroso and Del-Claro 2011).

Similarities and differences

There are several reasons to suspect eusocial insects should have higher DOL than social arachnids. In both eusocial insects and arachnids, DOL tends to increase with group size (Robinson 1992; Gautrais et al. 2002; Holbrook et al. 2011). This is possibly because, as colonies grow, they become more complex, and the profitability of streamlined workflow increases. While colony sizes in arachnids vary from two to several thousand individuals, colony sizes approach 100,000 in honeybees and more than 1,000,000 in some wasps, ants, and termites (Bourke 1999). Furthermore, eusocial insects need to perform numerous complex tasks that are wholly absent in arachnid societies, including active foraging for resources such as food, water, and nesting materials. This requires insect societies to be comparatively more active, and DOL may help to avoid resource bottlenecks. In contrast, arachnid societies passively wait for prey to become ensnared, and spiders produce their own nesting materials

endogenously. Both insect and arachnid societies engage in parental care. Finally, the lack of morphological castes in arachnid societies further conveys they may be limited in the level of task specialization that they can achieve. Despite these observations, studies on DOL in social arachnids have revealed surprisingly high levels of DOL (Holbrook et al. 2014; Wright et al. 2014). In fact, relative to their size, arachnid societies appear to have higher levels of task specialization than eusocial insects. One might argue that arachnid collective personalities are therefore comparatively more *orderly*—the one notable exception being the obligate sterility and reproductive division of labor that characterize the eusocial insects. Future studies on DOL and the mechanisms governing task specialization in both groups, and others, will help reveal any truly consistent differences in how they organize work, as well as its functional consequences.

Foraging, exploration, and boldness

Many recent studies have explored the collective foraging and exploratory tendencies of colonies. This is because foraging is something groups must do mostly outside their nest, and it is therefore easier to observe in intact colonies. Foraging is vital for colony growth and survival because it is how colonies acquire resources and discover new nesting locations. Boldness, on the other hand, is defined as the propensity of an individual to engage in risky behavior (Sloan Wilson et al. 1994). While *prima facie* it may seem that boldness bears no relation to foraging and exploration, these traits are often interdependent: foraging and exploration require leaving the safety of the nest, and thus present risk. In fact, boldness is often measured as the latency to enter a new environment, which is the necessary first step to exploration and foraging. It is therefore of little surprise that studies on collective personality regularly detect associations between these aspects of colony activity.

Eusocial insects

Inter-colony differences in foraging behavior have been documented in ants and bees, while wasps, termites, and other eusocial insects remain mostly absent from the literature. In harvester ants, for instance, colonies vary in their active foraging window: some colonies consistently begin foraging earlier each day, and cease foraging later than other colonies, which influences total resource intake and colony growth (Cole et al. 2008, 2010). This is directly related to the colony's genetic diversity. Other work has shown that the proximate mechanism driving these inter-colony differences may be related to how colonies regulate their foraging in response to environmental feedbacks (Gordon et al. 2011). However, colony survival is not always associated with higher overall foraging activity, at least in some species (Gordon 2013). In some species, it is colonies that exhibit *restraint* in foraging or greater fearfulness that enjoy the greatest fecundity (Gordon 2013; Blight et al. 2016).

The role of collective exploration in determining colony success is not well-known generally. Usually, exploration is tucked within a broader behavioral syndrome of other group behaviors, like aggressiveness or activity. Some studies, however, have linked inter-group foraging differences to differences in colony exploration and worker route learning ability (Pasquier and Gruter 2016). In fire ants, differences in exploratory behavior are correlated with foraging activity, and together predict colony growth in situ (Bockoven et al. 2015). In ants of the genus *Temnothorax*, success in competition for nests between species is determined by an interaction between colony exploratory tendencies. *Temnothorax longispinosus* performs best in rival house-hunting matches when their opponent (*T. curvispinosus*) has similar exploratory tendencies to their own. Conversely, *T. curvispinosus* tend to win contests for nests when their exploratory tendency is different from their own (Lichtenstein et al. 2015). A separate house-hunting study conducted in Argentine ants (*Linepithema humile*) observed colony-level differences in the speed and accuracy of collective nest relocation decisions; fast-deciding colonies were also more accurate (i.e., they chose nests of higher quality when given multiple alternatives) (Hui and Pinter-Wollman 2014).

Collective exploration is also thought to be a factor in biological invasions (Chapple et al. 2012; Carere and Gherardi 2013), possibly due to its effects on resource identification and enhanced competitive ability. In Argentine ants, colonies from introduced ranges tend to be more explorative, and more aggressive, than colonies in the species' native range (Blight et al. 2017). Boldness, like exploration, also frequently forms a syndrome with other group personality traits like exploration and aggressiveness, but collective boldness is not often directly measured in studies of collective personality. In at least one study, however, colony-level boldness was directly related to colony responsiveness to alarm pheromone, which could be an important component of colony defense (Chapman et al. 2011) and successful range expansion.

Studies on honeybees and bumblebees are often used for collective personality studies. Perhaps the most well-known example of honeybee collective behavior, and its consequences for fitness, is outlined in a study by Wray et al. (Wray et al. 2011). This study showed behavioral consistency in many colony-level traits, particularly collective foraging and defensive behavior. More defensive colonies were also better foragers, and this syndrome was positively correlated with both colony productivity and winter survival. There have been many studies detailing the genetic basis for collective traits such as foraging and aggressiveness in honeybees (Breed et al. 2004; Guzman-Novoa et al. 2004; Hunt 2007; Alaux et al. 2009), but Wray and colleagues demonstrated that these behaviors may be under strong selection, given that only 24% of new colonies survive their first winter in temperate climates (Seeley 1978). In bumblebees, inter-colony differences in collective foraging are linked with innate color

preferences and learning speed of workers (Raine and Chittka 2007, 2008), and colony foraging tendencies remain consistent over a colony's lifespan (Evans and Raine 2014). Lastly, anthropogenic factors, such as the use of agricultural pesticides, have been shown to negatively impact bumblebee collective foraging behavior, and potentially colony success (Gill et al. 2012). Exposure to such stressors provides one mechanism to explain non-adaptive differences in colony behavior, and their influence will likely only continue to grow.

Social arachnids

In arachnids, foraging behavior is the most well-studied aspect of collective personality. This is, in part, because the ability to subdue large prey has long been thought to underlie the evolution of sociality in these systems (Nentwig 1985; Lubin and Bilde 2007; Powers and Aviles 2007; Yip et al. 2008; Avilés and Guevara 2017; Pruitt and Avilés 2017). Unlike in the above sections on eusocial insects, collective exploration will not be considered here because social arachnids generally do not explore the environment beyond their webs in search of food. Individual and collective boldness, however, do appear to be linked to foraging efficiency in several social spiders. In *S. dumicola*, between-colony variation in the proportion of bold individuals present is positively related to both the speed and magnitude of collective foraging response to prey in the lab and field (Grinsted et al. 2013; Grinsted and Bacon 2014; Keiser et al. 2014; Keiser and Pruitt 2014; Wright et al. 2015; Lichtenstein et al. 2016b). Boldness in this species is also linked to the propensity to transmit cuticular bacteria to other nest mates (Keiser et al. 2016a), and the proportion of bold individuals within a colony can influence the ease with which bacteria spread throughout a colony (Keiser et al. 2017), including during collective foraging, which could determine a colony's vulnerability to disease outbreaks. Participation in web repair is also positively associated with individuals' boldness in *S. dumicola* (Keiser et al. 2016b). Boldness further determines the degree to which an individual spider will exhibit a "keystone" behavioral phenotype. Keystone individuals are defined as individuals that exhibit a large influence over group dynamics relative to their abundance (Modlmeier et al. 2014c). In *S. dumicola*, bold individuals catalyze greater task participation in shy colony members, leading to 400% more attackers and to an 80% decrease in latency to attack prey (Pruitt et al. 2013; Pruitt and Keiser 2014). However, not all populations are susceptible to keystone influence (Pruitt et al. 2017b). Thus, how individual-level personalities assemble together to generate collective personality appears to vary across sites, and is sometimes itself subject to site-specific selection (Modlmeier et al. 2014b; Pruitt et al. 2017b).

In *Anelosimus*, collective foraging aggressiveness can be determined by the presence of aggressive or bold individuals. Aggressive spiders are more likely to engage in prey capture,

attack more quickly, and secure prey more than their docile counterparts (Pruitt et al. 2008, 2012a; Holbrook et al. 2014; Wright et al. 2014), which makes colonies behave more aggressively in aggregate. Aggressive foraging behavior is likewise linked with individual boldness in several other *Anelosimus* spiders, such as *A. domingo* and *A. eximius* (Pruitt et al. 2011). Thus, across the *Anelosimus* genus, which contains more social species and independent origins of sociality than any other, individual-level personalities assemble seemingly additively in determining colony behavior (Agnarsson et al. 2006).

Similarities and differences

Insect and arachnid societies differ in the ways they acquire resources and interact with their environment. For example, eusocial insect societies are often initiated by one or sometimes a few individuals. Once a nesting site is chosen, foundresses must explore the environment for building materials and continually forage for food and water to produce eggs and feed young. When workers emerge, they take over foraging and defensive tasks. Foraging in eusocial insects is sometimes individualistic, where single foragers explore their surroundings for resources. However, once a resource is discovered, many species recruit others to help in transport. In social spiders, gravid females occasionally disperse long distances via “ballooning” (Schneider et al. 2001). This method of dispersal is passive and involves less explicit exploration. Likewise, rather than individually exploring their environment for resources, social spiders sit and wait for prey to become ensnared. For these reasons, studies on collective exploratory tendencies and activity level are almost absent in social spiders, and research instead focuses more on traits such as boldness and foraging aggressiveness toward prey. Other social arachnids, however, such as the social huntsman *Delena cancerides*, which actively hunt their prey, might be more amenable to studies focusing on collective foraging and exploration. This species hunts prey solitarily, like some species of wasps and ants, but occasionally shares some portion of this prey with fellow colony mates (Yip and Rayor 2011, 2013).

Collective exploration and boldness, however, may be more relevant in social spiders during the process of founding colonies via “bridging.” Bridging occurs when individuals send out strands of silk that anchor to a nearby bush (Schneider et al. 2001). Spiders then chain along these silken bridges and found a new colony together. It is unknown whether individual or colony-level boldness positively correlates with bridging behavior versus ballooning, or whether colony life history is associated with preferred dispersal routes. Habitat selection in many social arachnids is relatively unexplored, save for species that occupy limited real estate in rock cavities and under the bark of trees, like *D. cancerides* (Rowell and Aviles 1995).

Given the differences between eusocial insects and arachnids, these taxa provide a rich landscape for examining similarities and differences in collective personality. Linking personality with

meaningful variation among colonies in dispersal mode, growth rate, reproductive strategies, and aging remains a frontier and provides convenient links with the most prominent themes occurring in the literature on individual-level personalities, like the pace-of-life syndrome hypothesis (Biro and Stamps 2008).

Defensive behavior and aggressiveness

The ability of a colony to successfully defend itself, or defeat a rival in aggressive conflict, is often vital. Given the strength and ubiquity of predation and conflict as a selective force on animal societies, small differences in these traits can be instrumental in determining various outcomes (Davidson 1998; Rowles and O'Dowd 2007; Parr 2008; Cerda et al. 2013; Bengston and Dornhaus 2014).

Eusocial insects

In some *Temnothorax* ants, colonies composed of more aggressive individuals exhibit greater group defensive behavior against intruders (Modlmeier et al. 2014b), forage more effectively (Lichtenstein et al. 2016a), and are faster at nest relocation (Modlmeier et al. 2014b). Aggressive *Aphaenogaster* ant colonies are also better foragers, more thoroughly explore their environment, and are better intraspecific competitors compared to more docile colonies (Blight et al. 2016). However, high aggressiveness appears to be a double-edged sword: more aggressive *Aphaenogaster* colonies continue to forage at dangerously high temperatures, resulting in increased worker mortality rates (Blight et al. 2016).

Aggression also plays an important role in colony defense. More aggressive harvester ant colonies display less nest damage than less aggressive colonies, suggesting that they may be better defended (Wiernasz et al. 2014). Colonies of some ant species become more collectively aggressive when they encounter social parasites, such as slave-making ants. These forewarned colonies are less likely to be the target of slave raids and they lose fewer brood when raids occur (Kleeberg et al. 2014). *Temnothorax* colonies also vary in their collective aggressiveness depending on whether they are raised by their own queen or a parasitic slave-making queen (Keiser et al. 2015b), suggesting that developmental differences likely help determine inter-colony variation in collective aggressiveness. Lastly, the consequences of collective personalities also play a role in insect-plant mutualisms. A recent study showed that *Cecropia* trees harboring more aggressive *Azteca constructor* ant colonies suffered less leaf damage than trees harboring docile colonies (Marting et al. 2018). Other potential mutualisms that could be influenced by collective behavior have been hypothesized, such as that between paper wasps and weaver birds, but this has yet to be rigorously evaluated (Bologna et al. 2007).

Honeybees also display marked differences in collective aggressiveness (Collins et al. 1982; Breed and Rogers

1991; Breed et al. 2004), and colony aggressiveness and defensive behavior are positively correlated with foraging activity, which is linked to colony success. Colony-level defensive behavior is also influenced by the behavioral distribution of worker bees. One study showed that colonies composed of a 1:1 mixture of aggressive and docile bees displayed the most defensive behavior, but that colonies containing more individually aggressive bees are more hygienic than other compositions (Paleolog 2009). Such results convey that the links between the behavioral tendencies of individuals and groups are not always linear and intuitive. Honeybee colony aggressiveness can also be shaped by a few particularly aggressive workers (i.e., keystone individuals) that recruit more docile bees to attack intruders, as indicated in co-fostered colonies of European (docile) and Africanized (aggressive) bees (Guzman-Novoa et al. 2004).

Work on collective aggressiveness in social wasps is comparatively scant, and nonexistent in termites. However, it has been shown that inter-colony differences in aggressiveness are linked with queen behavioral type in paper wasps (*Polistes metricus*) (Wright et al. 2016b). Bold queens are more likely to remain on their nest after being repeatedly antagonized and give rise to workers that are also more likely to remain nest-bound when the colony is agitated. Conversely, shy queens tend to temporarily abandon their nest when agitated, but these queens produce aggressive workers that readily leave their nest to attack mock predators. Bolder queens also enjoy greater colony growth in the wild. Other insects that exhibit some degree of social organization also display group-level behavioral variation in defensive behavior, such as sheltering in domiciliary cockroaches when exposed to light (Planas-Sitja et al. 2015; Salazar et al. 2018), and evasion in pea aphids when exposed to predatory cues (Muratori et al. 2014). However, these represent more passive forms of defensiveness in comparison to other species that defend themselves aggressively.

The trend among many of these systems is that aggressiveness is an important driver of colony defense and competition against competitors. Another pattern emerging from these studies is that increased aggressiveness, while predictive of success in a wide variety of contexts, comes with costs. Colony aggressiveness may therefore regularly be under balancing selection in many insect systems. We therefore caution researchers when reporting the benefits of colony aggressiveness when only a narrow set of contexts is considered. Furthermore, researchers performing manipulation studies (particularly those occurring in the lab) that appear to discover “optimal” behavioral compositions should be skeptical regarding the ecological validity of their results, especially if these “optimal” compositions deviate greatly from those observed in nature.

Social arachnids

The ratios of behavioral types can determine the collective defensive behavior in several species of social spider. The webs of *A. studiosus*, can be expansive (several meters across), containing a rich community of heterospecific social parasites, ranging from kleptoparasites to colony-level predators (Agnarsson 2006; Perkins et al. 2007). Social parasite communities also increase in both abundance and richness with host colony size (Pruitt and Riechert 2011b) and negatively impact colony survival (Pruitt and Riechert 2011b). Aggressive *A. studiosus* colonies, while prone to infighting (Pruitt and Riechert 2009), are better defended against social parasite invaders (Pruitt and Riechert 2011b) and are more likely to respond to invaders (Pruitt and Riechert 2011b) and repel them (Pruitt and Ferrari 2011; Wright et al. 2014).

In *S. dumicola*, colonies are frequently raided by predatory ants from the genus *Anoplolepis* (Henschel 1998). *S. dumicola* colonies commonly experience high annual extinction rates of over 90% per year, and ant attacks can wipe out colonies in minutes (Wright et al. 2016a). In response, *S. dumicola* collectively spin walls of defensive silk to impede advancing ants (Wright et al. 2016a). Participation in defensive silk-spinning behavior is positively associated with individual boldness, yet colonies containing a mixture of bold and shy spiders exhibit over two times as much defensive silk-spinning behavior as monotypic colonies (Wright et al. 2016a). Here again, non-additive (i.e., synergistic) effects of group composition on collective personality appear to be common across many arthropod societies. Finally, many of the links between individual and collective personality seen in *Stegodyphus* disappear when colonies are subjected to prolonged predation risk, suggesting that some environments can remove the signature of collective personality by causing among-colony behavioral conformity (Wright et al. 2017).

Similarities and differences

Differences in the nest structures and individual morphology in eusocial insects and arachnids influences how these societies respond to predators, competitors, and disturbances to their colonies. Many eusocial insects can respond to a larger range of threats, from small arthropods to vertebrates, than can arachnids. This is owed to insects’ ability to leave their nests, *en masse*, with several thousand venomous, stinging, biting, and often flying, individuals to mob an intruder. Social arachnids are not so defended, as these societies are often smaller and less cohesive, and individuals are incapable of flying and stinging. Only a handful of studies have investigated defensive behavior in social arachnids (Pruitt 2013; Yip 2014; Keiser et al. 2015a; Wright et al. 2016a), whereas colony defensive behavior has been documented across a broad swath of eusocial insect taxa (Eisner et al. 1976; Judd 1998; Breed

et al. 2004). We therefore might predict stronger positive selection on collective defensive behavior in eusocial insects compared to arachnids.

Another difference between eusocial insects and arachnids is how they display aggressiveness. In arachnid societies, aggressiveness is often a reactive behavior in response to disturbance in their capture webs. Beyond this substrate, social spiders are unresponsive. In eusocial insect societies, however, aggressiveness is used both reactively against intruders and proactively against competitors and prey. We therefore might expect broader syndromes of correlated behavioral traits in association with aggressiveness and overall activity levels in eusocial insects as compared to arachnids, and that the situational costs and benefits of collective aggressiveness should be more pronounced.

One notable similarity between social spiders and ants appears to be trade-offs associated with aggressiveness. In ants, more aggressive societies tend to have increased foraging activity. While this appears to enhance resource acquisition, this also results in higher worker mortality due to overactive foraging in unfavorable environmental conditions (Gordon 2013). More cautious colonies that mitigate foraging in adverse conditions are commonly more successful. Similarly, in some spiders, aggressive colonies experience greater success in most contexts. However, aggressiveness comes with costs—aggressive colonies often cannibalize their own young, and do not provision young proficiently. In situ, mixed colonies enjoy greater overall fitness (Pruitt 2012). In the spider *S. dumicola*, a similar outcome occurs; aggressive colonies attack prey faster, and attack with more individuals than docile colonies (Keiser and Pruitt 2014; Wright et al. 2015). However, colonies of mixed composition exhibit twice as much defensive behavior when being raided by predatory ants (Wright et al. 2016a), which may explain why mixed compositions are most common in nature. We argue that such performance trade-offs associated with collective personality could be common across many social taxa, invertebrate or otherwise.

Decision-making, cognition, and learning

Between-individual variation in traits like cognition and learning might more appropriately be viewed as traits that *inform* personality, rather than being a personality trait *per se* (Carere and Locurto 2011; Griffin et al. 2015). Nevertheless, variation in collective cognition and learning are important when choosing nesting sites (Seeley and Buhman 1999; Mallon et al. 2001; Pratt et al. 2002; Passino et al. 2008; Sumpter and Pratt 2009), foraging (Beckers et al. 1993; Beekman et al. 2001), or possibly engaging in collective movements. Overall cognitive capacity is larger in collectives than individuals, suggesting that groups may be more adept at making optimal choices than individuals (Sasaki and Pratt 2012; Sasaki et al. 2013), and that this accuracy may scale with

group size. Different tasks performed within a colony might also have different cognitive demands, and thus cognitive ability could determine how efficient individuals and, in turn, their colonies are at executing particular tasks (Reznikova 2008). Some investigators have argued that colonies themselves might profitably be viewed as single cognitive units (Sasaki and Pratt 2018).

Eusocial insects

The bulk of studies investigating collective decision-making, cognition, and learning in eusocial insects comes from work on ants and bees. Colonies often must choose among nest sites that vary in quality depending on multiple attributes (Visscher 2007). In ants, while studies abound describing the processes involved in decision-making, from individuals up to their colonies, none to our knowledge have quantified between-colony variation in any cognitive trait. At least one study in *Temnothorax* ants, however, has demonstrated that nest relocation efficiency increases with increased colony aggressiveness (Modlmeier et al. 2014b), suggesting that collective personality represents another axis of decision-making strategies not captured by studies that evaluate group size alone. Yet, how aggressiveness may have influenced cognitive decision-making processes has not been investigated.

In honeybees, individual bees have been shown to differ widely in their cognitive and learning abilities using proboscis extension reflexes (Bitterman et al. 1983) and sucrose responsiveness (Scheiner et al. 1999, 2004). Honeybee learning ability can be affected by the presence of parasitic mites (Kralj et al. 2007), exposure to certain pesticides (Frost et al. 2013; Evans and Raine 2014; Stanley et al. 2015; Urlacher et al. 2016), and age (Scheiner et al. 2003). These individual differences frequently occur within the same colony, and likely help to determine colony-level behavior. At present, we know of no studies that have tested for colony-level differences in cognition in honeybees, or its possible effects on colony success or fitness. In bumblebees, however, different populations have been shown to exhibit differences in learning ability in response to rewarding stimuli (Raine et al. 2006; Ings et al. 2009). These differences in learning ability are correlated with differences in color preference, which has been shown to influence foraging performance and colony fitness (Raine and Chittka 2005). Additionally, higher learning speeds have been linked with increased foraging success in bumblebees (Raine and Chittka 2008). To what degree standard personality assays at the individual or colony level may enhance the predictability of inter-colony differences in learning and performance remains little examined.

In primates and several other mammals, there exists a positive relationship between brain size and group size (Dunbar 1992; Dunbar and Shultz 2007; Perez-Barberia et al. 2007; Street et al. 2017). One possible explanation for this has been

termed the *social brain hypothesis*, which posits that complex social life somehow requires comparatively complex, and thus larger, brains (Dunbar 1992). However, there are many alternative and non-mutually exclusive genetic (Montgomery et al. 2010), developmental (Finlay and Darlington 1995), ecological (Altmann 1998), and energetic explanations (DeCasien et al. 2017) that also need to be considered. In insects, however, no such general relationship (positive or negative) exists (Farris 2016), though it has been shown in some ant species (Kamhi et al. 2016). Instead of investing in individual cognition, social insects are thought to instead place emphasis on communication, which requires less brain investment (O'Donnell et al. 2015). This phenomenon is known as the *distributed cognition hypothesis* (Muscedere and Traniello 2012; Iliş et al. 2015; O'Donnell et al. 2015; Farris 2016). Presently, there are no studies investigating how such distributed communication systems may influence collective personality.

Social arachnids

Many have viewed arachnid behavior as being governed by instinct (Jackson and Cross 2011; Jakob et al. 2011). However, investigations hint that this is not always the case (Wilcox and Jackson 1998; Herberstein et al. 2013; Peckmezian and Taylor 2015). To what degree social living promotes greater or reduced cognitive ability, discussed above as the *social brain* and *distributed cognition hypotheses* (Dunbar and Shultz 2007; Perez-Barberia et al. 2007), and how this impacts collective learning in social arachnids, is unknown. Brain size however does not appear to differ between solitary species that differ in prey capture behavior, i.e., orb weaving vs. kleptoparasitism (Quesada et al. 2011). Studies on *S. dumicola* have shown that both individuals and whole colonies of spiders are capable of associative learning tasks using seismic cues (Holbrook et al. 2014; Pruitt et al. 2016). Furthermore, information can be transmitted from trained to untrained spiders at different rates depending on the behavioral type of demonstrators (Pruitt et al. 2016). This is the only study investigating links between learning, personality, and collective behavior in arachnids to date. Thus, many avenues remain open to exploration.

Similarities and differences

There are many reasons to suppose that selection on traits like collective cognition, learning, and collective decision-making should differ between eusocial insects and arachnids. Eusocial insects interact with their broader environments more intimately than arachnid societies in most respects. Thus, we might expect a higher capacity for collective learning and information transfer in eusocial insects relative to arachnids, especially in spatial and

visual learning and memory. We see evidence for this in bumblebees, where there is a link between individual and colony learning speed and visual memory (Raine and Chittka 2012). This variation is also linked with resource acquisition rates (Raine and Chittka 2007). Honeybees also have adept visual learning and memory (Zhang et al. 1999). When a new resource patch is discovered, individual workers gather information about the quality, distance, and direction of resources and communicate this information back to workers in a dance (Detrain and Deneubourg 2008). Similar information transfers occur when honeybee colonies relocate to new nesting sites (Seeley 1985; Seeley and Visscher 2004; List et al. 2009). Many ants likewise rely on spatial learning and memory in house-hunting and collective foraging (Mallon et al. 2001; Pratt et al. 2002; Detrain and Deneubourg 2008; Sumpter and Pratt 2009).

Arachnid societies, on the other hand, might perform as well as insects on associative learning and memory tasks, but tend to rely on seismic cues (Pruitt et al. 2016). Social arachnids have poor eyesight; thus, visual learning tasks are likely not relevant for this system. Studies on collective cognition in arachnids are needed to determine how/whether group cognitive ability scales with group size, as seen in some eusocial insects. While many studies have linked individual personality with learning styles (Bebus et al. 2016; Medina-Garcia et al. 2017; Nawroth et al. 2017; Shaw and Schmelz 2017), the intersection of collective personality and group cognition in virtually any taxon remains a wide-open field.

Nest construction

One of the most impressive collective behaviors of social arthropods is cooperative nest-building. These nest structures can vary widely in size and shape, from small inconspicuous piles of sand blocking nest entrances in *Temnothorax* ants, to large termite mounds that reach heights of 4 meters or more (Bignell et al. 2011a, b). In arachnids, webs can vary in size from small structures a few centimeters across to massive blanket-like webs spanning several meters in diameter. The building of many of these structures is a self-organizing process, where higher-level patterns emerge from the interactions between individuals eliciting both positive and negative feedback responses. These responses are mediated indirectly by *stigmergy*, a process where modifications of the environment by one individual stimulate the performance of a second modification by others (Camazine 1991; Karsai and Penzes 1993; Theraulaz and Bonabeau 1995; Bonabeau et al. 1997; Theraulaz et al. 1998a, 2002). The presence of such feedback mechanisms, and variability in them, likely underlie the variability in collective behavioral tendencies seen in many eusocial insects and possibly arachnids (Table 1). Despite the

Table 1 A survey of foundational and well-established hypotheses on collective personalities

| Hypothesis | Collective personality trait | Temporal scale | Taxa | Source |
|--|-----------------------------------|--------------------------------|-------------------------|--|
| H1: Groups exhibit stable differences in collective behavior | Collective aggressiveness | Days | Ants | Lichtenstein et al. (2015), Marting et al. (2018), Wiernasz et al. (2014) |
| | | | Spiders | Pruitt et al. (2013), Pruitt and Keiser (2014) |
| | | Weeks | Ants | Bengston and Dornhaus (2014), Blight et al. (2017), Scharf et al. (2012) |
| | | | Bees | Wray et al. (2011) |
| | | | Ants | Blight et al. (2016, Blight et al. 2016), Buczkowski & Silverman (2006), Crosland (1990) |
| | Exploratory and foraging behavior | One year | Bees | Pearce et al. (2001) |
| | | | Ants | Suarez et al. (2002) |
| | | Days | Ants | Marting et al. (2018), Gordon et al. (2011), Lichtenstein et al. (2015) |
| | | | Bees | Raine and Chittka (2008) |
| | | | Fish | Jolles et al. (2018) |
| | Nest repair/relocation | Weeks | Ants | Bengston and Dornhaus (2014), Blight et al. (2017), Bockoven et al. (2015), Scharf et al. (2012) |
| | | | Bees | Wray et al. (2011) |
| | | Months | Ants | Blight et al. (2016, Blight et al. 2016) |
| | | | Ants | Cole et al. (2010), Gordon et al. (2013) |
| | | Days | Ants | Cronin et al. (2015) |
| H2: The personality scores of group members determine the collective personality of the group | Collective aggressiveness | Aggressiveness | Ants | Modlmeier et al. (2014a) |
| | | | Bees | Rittschof (2017) |
| | | Boldness | Wasps | Wright et al. (2017) |
| | | | Spiders | Pruitt et al. (2013), Pruitt and Keiser (2014), Pruitt & Pinter-Wollman (2015), Wright et al. (2015) |
| | | | Fish | Brown & Irving (2013), Jolles et al. (2017) |
| | Exploratory and foraging behavior | Activity level and sociability | Lepidopterans | Dussutour et al. (2008) |
| | | | Fish | McDonald et al. (2016) |
| | | Exploratory behavior | Birds | Aplin et al. (2014) |
| | | | Slime molds | Vogel et al. (2015) |
| | | | Termites | Mizumoto et al. (2015) |
| | Nest repair/relocation | Activity level | Ants | Modlmeier et al. (2014b) |
| | | | Ants | Hui and Pinter-Wollman (2014) |
| | | Aggressiveness | Ants | Modlmeier et al. (2014b) |
| | | | Ants | Hui and Pinter-Wollman (2014) |
| | | | Ants | Hui and Pinter-Wollman (2014) |
| H3: Collective personality predicts colony performance | Collective aggressiveness | Performance metric | Contests over resources | Bengston and Dornhaus (2014), Blight et al. (2016), Lichtenstein et al. (2015) |
| | | | Colony mass | Wray et al. (2011) |
| | | Damage to nest | Spiders | Pruitt et al. (2016), Pruitt and Keiser (2014) |
| | | | Ants | Wiernasz et al. (2014) |
| | | | Ants | Wiernasz et al. (2014) |

Table 1 (continued)

| Hypothesis | Collective personality trait | Temporal scale | Taxa | Source |
|--|-----------------------------------|---------------------------|---------|--|
| | | Host plant health | Ants | Marting et al. (2018) |
| | | Repelling parasites | Ants | Jongepier et al. (2014), Pamminer et al. (2011, 2012) |
| | | Survival and reproduction | Spiders | Pruitt et al. (2015) |
| | Exploratory and foraging behavior | Contests over resources | Ants | Bengston and Dornhaus (2014), Blight et al. (2016), Lichtenstein et al. (2015) |
| | | Colony mass | Bees | Wray et al. (2011) |
| Hypothesis | Collective personality trait | Life history trait | Taxa | Source |
| H4: Collective personality shapes colony life history | Aggressiveness | Productivity | Ants | Bengston et al. (2017), Blight et al. (2016), Bockoven et al. (2015), Scharf et al. (2012) |
| | | Reproductive investment | Ants | Bengston et al. (2017) |
| | Exploratory and foraging behavior | Productivity | Ants | Bengston et al. (2017), Blight et al. (2016) |
| | | Reproductive investment | Ants | Bengston et al. (2017) |
| | Nest repair/relocation | Productivity | Ants | Scharf et al. (2012) |

variation in nests observed between species, and even within species, studies testing for consistent between-colony differences in nest architecture that control for environment are limited.

Eusocial insects

Between-colony variation in nest construction behavior in eusocial insects has been observed in only a handful of studies. *Temnothorax rugatulus* prioritizes nests with small openings, as these are often more easily defended (Visscher 2007). When a nest has unsuitably wide entrances, *T. rugatulus* workers will retrieve small grains of sand and other debris which they then use to wall-in the exposed areas of their crevice. Researchers have found that individual colonies differ consistently in the wall architectures that they construct both across environments and repeated building events (DiRienzo and Dornhaus 2017). The subterranean termite, *Reticulitermes speratus*, builds shelter tubes that protect individual termites while foraging. When researchers split larger colonies into smaller sub-colonies and observed their shelter tube-building, they found that sub-colonies from the same source colony built similarly patterned tubes that were distinct from the tubes built by sub-colonies created from other colonies (Mizumoto and Matsuura 2013). These differences can be attributed to the degree of positive feedback exhibited, as well as the number of termites actively building the

structures (Mizumoto et al. 2015). More studies are needed to understand the mechanisms driving nest variation across colonies, as well as their performance implications.

Social arachnids

No current studies exist addressing collective personalities and the types/shapes/sizes of webs groups collectively spin. However, we know from a study in *A. studiosus* that webs constructed by aggressive individuals retain prey 64% longer than webs constructed by docile spiders (Wright et al. 2014). In *S. dumicola*, the shape of the substrate architecture available to construct capture webs influences both the mean and repeatability of collective foraging behavior across colonies (Modlmeier et al. 2014a), conveying that physical differences in the surrounding environment impacts the collective behavior that groups exhibit. Future studies that more finely quantify aspects of web architecture in association with colonies' collective behavioral type are still needed.

Similarities and differences

There are currently too few studies investigating the role of group personality in eusocial insect and arachnid nest construction to produce any meaningful comparisons. Yet, the number of plausible interesting relationships between collective personality and nest-building behavior

Table 2 Questions, themes, and hypotheses

| General question | Specific hypotheses |
|---|---|
| Q1: In colonies that experience fission-fusion dynamics, how do the personalities of groups change as they divide or merge? | <p>Hypothesis 1a: In social species whose colonies fragment, daughter colonies will initially resemble their mother colony in collective personality.</p> <p>Hypothesis 1b: Daughter colonies will develop distinct collective personalities, which predict division of labor within the super-colony.</p> <p>Hypothesis 1c: Variation in collective personality between the nests of a single polydomous colony can change to benefit the super-colony, akin to division of labor across multiple nests.</p> |
| Q2: Do colonies' collective behaviors determine non-linear relationships between colony mass and metabolism? | <p>Hypothesis 2a: The presence of seemingly inactive "lazy individuals" will reduce colony metabolic rate and collective activity level.</p> <p>Hypothesis 2b: The metabolic rate of active colonies will scale like single organisms, whereas the metabolic rates of inactive colonies will plateau at a shallower threshold.</p> <p>Hypothesis 2c: The presence of inactive individuals will be locally adapted (perhaps in patchy resource areas), driving geographic variation in metabolic scaling patterns driven by collective personality.</p> |
| Q3: Does colony personality influence collective cognition/learning? | <p>Hypothesis 3a: Groups will differ in their collective cognitive capacity based on the cognitive capacities of individual constituents.</p> <p>Hypothesis 3b: Groups will differ in collective learning based on the distribution of learning types within the group (e.g., proportion or presence of associative vs. spatial learners).</p> <p>Hypothesis 3c: Groups will perform better at certain tasks based on the learning types they contain. For instance, spatial learners might be better foragers, whereas associative learners might defend their colonies more closely.</p> <p>Hypothesis 3d: Mixed colonies will benefit from having a diversity of learning types, based on environmental/population differences such as food abundance or threat level.</p> <p>Hypothesis 3e: The presence of one or a few individuals of high cognitive ability will be sufficient to drive fast collective learning rates and low error rates for the group.</p> |
| Q4: Do groups exhibit consistent differences in their decision-making strategies? | <p>Hypothesis 4a: Different colonies will consistently tend to favor <i>speed</i> over <i>accuracy</i> and vice versa during migrations to new nests.</p> <p>Hypothesis 4b: Different colonies will consistently tend to favor <i>cohesion</i> over <i>speed</i> and vice versa during migrations to new nests.</p> <p>Hypothesis 4c: Low nest competition will favor high accuracy, which will require more time, and high competition favors high speed.</p> |
| Q5: Can autocorrelation of group-level personality be used as an indicator of incipient group collapse? | <p>Hypothesis 5a: Groups will exhibit stable colony personalities across their lifespans with some stochastic variation and predictable seasonal variation.</p> <p>Hypothesis 5b: The emergence of reduced temporal autocorrelation or increased within-colony variance in personality will signal the collapse or disbanding of a group.</p> <p>Hypothesis 5c: The emergence of reduced temporal autocorrelation or increased within-colony variance in personality will precede other indicators of colony collapse such as increase internal violence, decreased nest maintenance, and decreased reproductive rate.</p> <p>Hypothesis 5d: Across the lifespans of colonies, predictable patterns in collective personality will emerge.</p> |
| Q6: Do collective personalities of colonies determine their interior carrying capacity and population biology? | <p>Hypothesis 6a: Colonies will have internal carrying capacities and intrinsic growth rates specific to colonies that depend on their collective personalities.</p> <p>Hypothesis 6b: The collective personality of colonies will determine their intra-colony intrinsic growth rate and carrying capacity.</p> <p>Hypothesis 6c: Colonies with low intra-colony carrying capacities and intrinsic growth rates will grow and reproduce less readily.</p> <p>Hypothesis 6d: Populations composed of colonies with low carrying capacities and intrinsic growth rates will be more stable, will reach higher densities of colonies, and be less likely to overshoot their population carrying capacity.</p> |
| Q7: Can parasites shape colony personality to increase parasite reproduction and dispersal? | <p>Hypothesis 7a: Social parasites will manipulate the collective behavior of groups to further their own propagation (increase affinity to foreign conspecifics, decrease colony aggressiveness so more parasites can infect colony, increase exploration so parasites can propagate easier, etc.).</p> <p>Hypothesis 7b: Infected colonies will differ behaviorally from uninfected colonies, and this difference in collective behavior increases the infection risk of neighboring colonies and increases host colony competence.</p> |
| Q8: Do colonies' collective personalities influence associated inquiline communities? | <p>Hypothesis 8a: Non-aggressive colonies will foster more inquilines and associated animal life, thereby destabilizing the colonies.</p> <p>Hypothesis 8b: Aggressive colonies will repel inquilines, and consequently will not benefit from potential mutualistic interactions with inquilines.</p> |

Table 2 (continued)

| General question | Specific hypotheses |
|---|---|
| | <p>Hypothesis 8c: Colonies with moderate aggressiveness and greater intracolony behavioral diversity will foster an intermediate load of inquilines that involve more mutualistic interactions.</p> <p>Hypothesis 8d: Colonies of intermediate aggressiveness and mutualistic interactions with inquilines will be more temporally stable than extremely aggressive and docile colonies.</p> |
| Q9: To what degree does the evolution of colony personality mimic the evolution of individual-level traits? | <p>Hypothesis 9a: The heritability of colony personality is greater in colonies that operate more as a single selective unit (e.g., highly eusocial societies, inbred groups) or in instances where societies are established by a single or group of related foundresses.</p> <p>Hypothesis 9b: Among-group variation in collective personality and the effectiveness of selection on it positively co-varies with the level of genetic divergence across groups</p> <p>Hypothesis 9c: Negative frequency-dependent selection and cross-contextual trade-offs associated with colony personality act to maintain heritable variation in colony traits within populations.</p> <p>Hypothesis 9d: Colonies surrounded by neighbors of unlike collective personality will compete less for resources, and increase the collective performance of that neighborhood of colonies.</p> <p>Hypothesis 9e: Through time, neighboring colonies will exhibit stronger differences in their collective personalities to adopt distinct niches and reduce competition across societies.</p> |
| Q10: Colony personality and queen number and behavior: are polygynous colonies (multiple queens) more aggressive than monogynous colonies (single queen) towards intruders? | <p>Hypothesis 10a: Workers from polygynous colonies will be less aggressive to foreign queens and other intruders.</p> <p>Hypothesis 10b: Polygynous colonies will be more willing to accept and rear foreign queens than monogynous colonies, due to reduced overall collective aggressiveness.</p> <p>Hypothesis 10c: Polygynous colonies will be more susceptible to parasitism by inquilines.</p> |
| Q11: How does collective personality determine tolerance/affinity of neighbors? | <p>Hypothesis 11a: Presence of highly aggressive colonies members will increase collective aggressiveness of colonies, and yet aggressive individuals will be more likely to perish in fights between colonies.</p> <p>Hypothesis 11b: On a short time scale, aggressive interactions between colonies will decrease collective aggressiveness by depleting aggressive individuals.</p> <p>Hypothesis 11c: Colonies that quickly create aggressive individuals and recover their collective aggressiveness will outcompete colonies still depleted of aggressive individuals.</p> <p>Hypothesis 11d: Cycles of colonies depleting and replenishing aggressive individuals will lead to arms race to create more and more aggressive colonies.</p> <p>Hypothesis 11e: Colonies with very low aggressiveness may outperform aggressive colonies when aggressive colonies are at high representation, because they avoid the cost of inter-group conflict, akin to a colony level hawk-dove game</p> |
| Q12: How does collective personality relate to the social responsiveness or social susceptibility of its members? | <p>Hypothesis 12a: The social responsiveness of a colony will depend on the behavioral distribution of its individuals. Certain behavioral types (e.g. docile or shy types) will be more responsive to fellow group members than others.</p> <p>Hypothesis 12b: The behavioral types that are socially responsive to the behavior of fellow colony members (e.g., shy individuals) may not be the most socially responsive to individuals from other colonies (e.g., aggressive individuals).</p> <p>Hypothesis 12c: Colonies' social responsiveness will have a concave-down relationship with state (starvation level, condition, infection status): small reductions in colony condition will increase social responsiveness before reaching such threshold where responsiveness to fellow colony members and enemies alike will drop off dramatically.</p> |
| Q13: How does collect personality influence horizontal transmission of group members across colonies? | <p>Hypothesis 13a: Less collectively aggressive colonies will be more likely to exchange individuals, whereas aggressive colonies will be more likely to retain members and repel interlopers.</p> <p>Hypothesis 13b: The transmission of individuals between colonies will erode between-colony behavioral variation.</p> <p>Hypothesis 13c: Polydomous (multi-nest) colonies will exchange more individuals than monodomous colonies, thereby homogenizing inter-subcolony behavioral variation.</p> |
| Q14: Can colony mortality and collective behaviors form positive feedback loops? | <p>Hypothesis 14a: Colonies that exhibit a reduced tendency to forage, defend themselves, or engage in hygienic behaviors will suffer increased mortality of colony members.</p> <p>Hypothesis 14b: The mortality of colony members will reduce collective foraging, defense, and hygienic behaviors at the colony level, and may bias the representation of personality types in the remaining members.</p> <p>Hypothesis 14c: Mortality of group members and reduced collective foraging, defense, and hygienic behavior will form positive feedback cycles that lead to colony collapse.</p> |

Table 2 (continued)

| General question | Specific hypotheses |
|---|--|
| | <i>Hypothesis 14d:</i> The beginning of this feedback cycle will generate reduced temporal autocorrelation and increases in within-colony variance in collective personality, foretelling of imminent collapse. |
| Q15: Does social heterosis (i.e., within-colony behavioral diversity) generate variation in the flexibility of collective behavior? | <i>Hypothesis 16a:</i> Diversity in member colony personality will beget greater behavioral flexibility in collective behavioral tendencies. <i>Hypothesis 16b:</i> Colonies with more flexible collective personalities will prove more successful at exploiting a range of resources and conditions, whereas more consistent colonies will before better than flexible colonies only under a narrow range of environmental conditions. <i>Hypothesis 17c:</i> Stable environments will select for behavioral consistency in collective personality, whereas dynamic environments will favor greater plasticity in collective personality. |
| Q16: How does collective personality shape patterns of niche construction by large colonies? | <i>Hypothesis 17a:</i> The collective personality of large social arthropod colonies will change how they alter local ecosystem or community properties (e.g. deposits of nutrients, excessive nest structures, or inquiline communities). <i>Hypothesis 17b:</i> Such alterations to local environments will favor the performance of certain collective behavioral phenotypes, often of the phenotypes of the colonies that made them. <i>Hypothesis 17c:</i> When a collective behavioral phenotype alters the local environment, and the local environment in turn favors that collective behavioral phenotype, can generate a feedback loop. <i>Hypothesis 17d:</i> Behavior vs. local environment feedback loops could generate behavioral correlations. For instance, intense collective foraging may create large midden heaps, which might attract parasites or predators, and this might favor collective aggressiveness. This result would be a correlation between collective foraging and collective aggressiveness. |

are countless. Thus, this topic remains a unique niche and opportunity for new researchers.

Future directions

By comparing our understanding of 10 aspects of collective personality in eusocial and arachnid societies, we shed light on many unknowns in the literature on collective personality, as well as emphasize that numerous key questions remain unanswered. For instance, in groups that experience fission-fusion dynamics, how might collective personalities change as groups fractionate or merge? How often does collective personality influence group cognition or decision-making? Can parasites modify or exploit the collective behavior of groups to the parasite's advantage, similar to the way some parasites manipulate the behavior of individuals (Lefevre et al. 2009; Andersen et al. 2012)? More broadly, does variation across social taxa in social structure (e.g., temporary/facultative/obligate sociality, communal, subsocial, and eusocial) generate predictable variation in the types of personality exhibited by individuals or groups, or their distributions? And the list goes on. We catalog here questions, themes, and hypotheses (summarized in Table 2) that should be addressed in the near future to help take a broader perspective on this topic. Our ultimate goal is to forge links between the literature on collective personality and other fields in evolutionary behavioral ecology beyond what the literature has already reasonably established (Table 1). While this list is by no

means exhaustive, it is meant to inspire researchers to think diversely and creatively about how collective personality stands to influence the way groups function, and how groups interact in a broader ecological context.

Our review also highlights that many studies have linked collective personality with colony performance (Table 1), but surprisingly, very few of these studies have been conducted in situ. Yet, field studies are likely to be illuminating (and essential) because they can reveal situational costs and benefits to colonies' collective behavioral tendencies that are obscured in lab environments.

Finally, we argue that by approaching collective personality traits with the same framework that evolutionary behavioral ecologists approach individual traits, we are likely to enhance our understanding of how and why collective behavioral traits evolve in contrasting environments (e.g., costs vs. benefits), how they interact with colonies' life history and niche, and the degree to which such traits can respond to selection (Table 2). Collective personality, as a framework, has the potential to inform our understanding of how selection acts on intraspecific variation in collective phenotypes, which in turn has given rise to much of the variation in collective behavior observed across arthropods societies (and potentially beyond) today. If we have succeeded, this review will serve as an updated roadmap and compass for those interested in pushing the field of collective personalities forward.

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