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Personality in social insects: How does worker personality determine colony personality?

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Abstract Social insect colonies and the workers comprising them, each exhibit consistent individual differences in behavior, also known as ‘personalities’. Because the behavior of social insect colonies emerges from the actions of their workers, individual variation among workers’ personality may be important in determining the variation we observe among colonies. The reproductive unit of social insects, on which natural selection acts, is the colony, not individual workers. Therefore, it is important to understand what mechanisms govern the observed variation among colonies. Here I propose three hypotheses that address how consistent individual differences in the behavior of workers may lead to consistent individual differences in the behavior of colonies: 1. Colonies differ consistently in their average of worker personality; 2. The distribution but not the average of worker personalities varies consistently among colonies; and 3. Colony personality does not emerge from its worker personality composition but from consistent external constraints. I review evidence supporting each of these hypotheses and suggest methods to further investigate them. The study of how colony personality emerges from the personalities of the workers comprising them may shed light on the mechanisms underlying consistent individual differences in the behavior of other animals [*Current Zoology* 58 (4): 579–587, 2012].

Keywords Insect, Colony, Personality, Worker

1 Introduction

Eusocial insects live as complex systems comprised of two levels of organization: workers and colonies. In most ant species, and in some bee and wasp species, workers are sterile and only the queens lay eggs, producing more workers. Queens depend on the workers for food and defense. The more resources workers retrieve, the more workers a queen can produce, and a colony can sustain, creating a positive feedback loop on colony size that is limited by the environment. A colony reproduces by producing more queens that found new colonies. Thus, natural selection acts at the colony level, on variation among colonies, not on variation among workers. Still, the action of workers determines whether or not a colony will have enough resources to produce more queens (for more information on the social organization of ants see Holldobler and Wilson 1990).

The behavior of social insect workers is self-organized and no single individual directs the work of others. Workers follow local rules that result in the regulation of colony activity. What we view as colony level behaviors (e.g., producing queens that will form new colonies) is an emergent property of the workers’ actions. For example, workers use local cues such as pheromone trails to obtain food (Morgan, 2009), and social cues to collectively choose a new nest site (Seeley, 1995; Franks et al., 2002).

Personality is defined as consistent individual differences in behavior across time and/or situations (Wilson et al., 1994; Gosling, 2001; Sih et al., 2004; Reale et al., 2007). Thus, personality is a multidimensional combination of highly correlated behaviors (Mather and Anderson, 1993). In social insects, both workers and colonies exhibit personalities. Individual workers may differ consistently in their behavior across time and situation. For example, certain workers may interact more with other individuals, i.e., be more sociable (Reale et al., 2007) when foraging and when taking care of brood, i.e., across situations, while other workers may avoid other individuals when performing any task. Colonies also differ from one another in a consistent manner across situations, i.e. have personalities. For example, a certain colony may always have more workers outside the nest in any situation (e.g., foraging or disturbance) than another colony that has only few workers out of the nest in any situation. Constraints introduced by personality traits may provide a selective

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advantage in certain situations but a disadvantage in others (Sih et al., 2004). For a review of such trade-offs in an invertebrate system, see Pruitt and Riechert (2012), in this issue. In social insects, a colony that sends out many workers will gather more food but will also lose more workers to predation than a colony in which only few workers leave the nest. Because natural selection acts on colonies, behavioral variation at the colony level will determine which colonies will persist and reproduce in a given population.

Much work on the behavior of social insects has been devoted to understanding the distribution of workers among tasks. At any given moment, each worker can perform only one task, but the colony as a whole performs many tasks simultaneously. So tasks are divided among workers and not all workers perform the same task at any given time. Workers may specialize in performing certain tasks (Robson and Traniello, 1999), or switch often among tasks as they age (i.e., temporal polyethism: (Calderone, 1995; Gordon et al., 2005; Seid and Traniello, 2006; Camargo et al., 2007)), or in response to environmental changes (Gordon, 1989; Gordon, 1996). The allocation of workers to various tasks depends on external cues, such as interactions among ants and changes in the environment (Gordon, 1996), and on internal cues such as morphology (Oster and Wilson, 1978) and gene expression (Ben-Shahar et al., 2002). Studies of individual variation in behavior among social insect workers often focus on the difference between individuals that perform only one task, also called specialists, and those that perform many tasks, called elites (Robson and Traniello, 1999).

Here I will not discuss how workers are allocated to various tasks or whether or not workers specialize in certain tasks. The term ‘worker personality’ in this paper does not concern which task a worker performs or the number of tasks it performs. By ‘worker personality’ I refer to a measure of how a worker performs any task. For example, an active worker will perform much of any task, whereas an inactive worker will perform very little of any task. Both active and inactive workers may perform only few tasks or many tasks throughout their lifetime, but how many and which tasks they perform are different questions from the focus of this paper, which is how they perform the different tasks, or, what is their personality.

Colony personality refers to the consistent individual differences among colonies in how they behave across different situations. This individual variation is not in how much of each task a colony performs (e.g., how much foraging or how much brood care) but in how the colony performs and regulates these tasks. For example, colonies of the harvester ant *Pogomomyrmex barbatus* vary consistently in the baseline numbers of foragers that leave the nest to collect seeds and this variation correlates with the baseline number of patrollers that leave the nest each morning to explore foraging sites for the day (Gordon et al., 2011). *Messor andrei* harvester ant colonies vary consistently in how fast they retrieve seeds to the nest which corresponds to how fast they remove debris away from the nest mound (Pinter-Wollman et al., 2012). Honey bee, *Apis melifera*, colonies show consistent individual variation in foraging activity, defensive response, and undertaking, all of which correlate with one another (Wray et al., 2011). The way I use the term colony personality here corresponds to the definition of the term in other studies of animal personalities which ask whether an animal is more or less active in both foraging and mate choice situations and not whether an animal performs more mating or more foraging (Reale et al., 2007).

The behavior of social groups is determined by the personalities of the individuals comprising them (Crosland, 1990; Sih and Watters, 2005; Paleolog, 2009; Kurvers et al., 2010; Pruitt and Riechert, 2011). Therefore, it is likely that colony personality too emerges from the aggregation of the personalities of the workers that comprise it. Here I propose three testable hypotheses that suggest how colony personalities might emerge from the action of the workers comprising them: 1. Colonies differ consistently in their average of worker personalities; 2. The distribution of worker personalities varies consistently among colonies; and 3. Worker composition does not determine colony personality, instead external constraints, that consistently affect colony behavior, vary among colonies.

To explain each of these hypotheses, I will use as an example the regulation of colony foraging activity in the red harvester ant *P. barbatus* (Gordon, 2010). This ant species lives in arid environments in the southwest of the United States. Colonies regulate their activity throughout the day because when temperatures increase, workers outside the nest, such as foragers, patrollers, and midden workers, are in danger of desiccation. Workers of this species follow simple local rules to decide whether or not to leave the nest (Gordon, 2002). For example, the return rate of successful foragers determines whether or not a worker will leave the nest to forage (Schafer et al., 2006). Colonies vary in both their baseline foraging rate and in how they regulate foraging activity when responding to changes in the environment (Gordon et al., 2011). The rates at which patrollers and foragers leave the nest, are correlated within a colony and vary among colonies (Gordon et al., 2011), thus producing a colony level personality trait. The hypotheses I suggest here address how consistent variation in the regulation of colony activities emerges from the local rules followed by the workers comprising the colony. For simplicity, these local rules will exemplify worker personalities, even though it still remains to be shown that workers follow the same rules in more than one situation. Variation among colonies in regulation of foraging may lead to variation in colony survival and reproductive success.

1.1 Colonies vary in average worker personality (different average, similar distribution)

My first hypothesis proposes that colonies vary in personality because of differences in average worker personalities (Figure 1A). According to this hypothesis colonies do not vary in the distribution of worker personalities, but in the mean worker personality within each colony. For example, activity is one of five animal personality traits according to Reale et al. (2007) so a colony comprised mostly of active workers might respond faster to changes in its environment than a colony comprised of workers that are not active. This hypothesis suggests that colony personality emerges from the average personality of its workers.

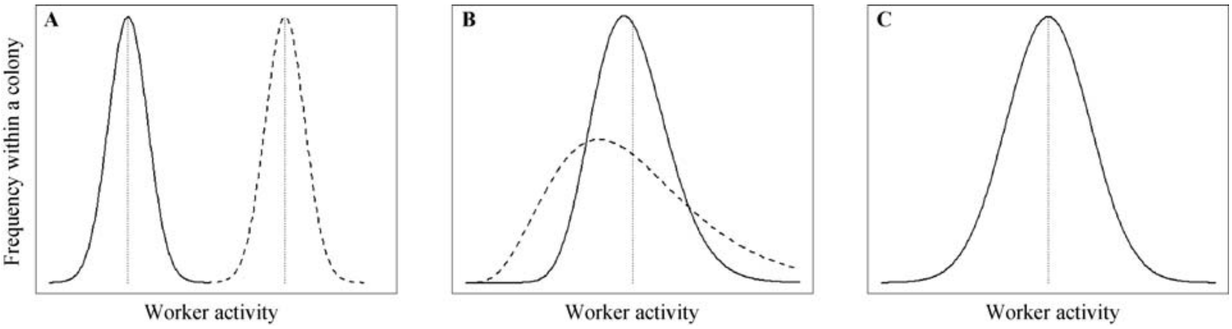

Fig. 1 Frequency of worker personalities within a colony
As an example of worker personality (x axis), I use worker activity. All vertical dotted lines indicate the average activity of all workers in a colony. **A**. Colonies vary in average worker activity. The dashed line represents a colony that will respond quickly to rapid environmental changes because most of its workers are highly active; the solid line represents a colony that might be slower to respond to environmental changes because most of its workers are not very active. In this case colony personality emerges from the average personality of its workers. **B**. Colonies vary in the distribution shape of worker activities, but not in average worker activity. The dashed line represents a colony that will respond to a larger range of environmental conditions due to its large variance in worker activity. The solid line represents a colony that will respond only to a narrow range of environmental conditions because workers are less variable in their activity levels. **C**. Colonies do not differ in the distribution or in the average of worker activity; instead external features (discussed in the text) determine colony personality.

Applying this hypothesis to the example of foraging regulation of *P. barbatus* one might predict that colonies vary in their regulation of foraging because all workers in each colony follow the same local rule when deciding whether or not to leave the nest, and colonies vary in this local rule. For example, all workers in one colony leave the nest if they encounter at least 0.6 returning foragers per second, while all workers in another colony leave the nest if they encounter at least 1.2 returning foragers per second. The second colony will thus be more sensitive to changes in the return rate of its foragers (Gordon et al., 2011).

Studies show that certain group behaviors emerge from the average behavior of the workers, suggesting that average worker personality may determine colony personality. For example, the cleanness of honeybee nests is determined by the number of hygienic bees; There is a positive relationship between the number of dead brood cells that are removed from the nest and the number of hygienic bees in the group (Paleolog, 2009). Colony defense behavior of *Rhytidoponera confuse* ants is determined by average worker aggression; the number of highly aggressive individuals in a colony is positively related to the overall colony aggression (Crosland, 1990). How fast a colony of *Temnothorax albipensis* ants finds a new nest site depends on the average experience of its workers (Langridge et al., 2008). Variation among *Bombus terrestris* bumble bee colonies in the average bee preference towards the color violet results in variation among colonies in nectar stores which can affect reproductive success (Raine and Chittka, 2007).

1.2 Colonies vary in worker personality distribution (similar average, different variance)

This hypothesis suggests that colonies vary in personality because their distribution of worker personalities varies, but not the average of their worker personality (Fig. 1B). According to this hypothesis different colonies may consist of similar worker personalities, i.e., overlapping worker personality ranges and average worker personalities, but they vary in the frequency, or representation, of each worker personality. For example, one colony may have few highly active workers and many workers that are not very active (i.e., a skewed distribution, see dashed line in Fig. 1B). Another colony will be comprised of workers that all exhibit a medium level of activity (i.e., normal distribution, see solid line Fig. 1B). The colony with a skewed worker activity distribution might have an advantage over the other colony when faced with time-sensitive tasks that require only few active workers to complete, e.g., depletion of an ephemeral food source where competition is strong. In contrast, the colony with a normal distribution of worker activity might have an advantage over the other colony when continuous work is needed, e.g., when foraging for an abundant food like seeds. Note that in this situation the personality of a colony is not simply the average personality of its workers.

In our example of *P. barbatus* foraging regulation, this hypothesis predicts that colonies will vary in the distribution of return rates that elicit foraging response, but on average, these return rates will be similar in all colonies. For example, in one colony, most individuals will leave the nest to forage when foragers return at a rate of at least 0.8 ants per second. However, in another colony a third of the workers respond to a return rate of at least 0.4 ants per second while two thirds of the foragers respond to a return rate of at least one returning ant per second. Thus, most of the time, the later colony will be more sensitive to changes in its environment than the first colony, but when the few workers who respond to lower return rates are active, the regulation of foraging activity in the second colony will be less sensitive to changes in forager return rate. The second colony will likely exhibit more day-to-day variation in foraging regulation than the first colony.

Studies show that the distribution of personalities within a group of social insects indeed determines the group behavior as a whole. Honeybee groups comprised of half gentle and half defensive bees were as aggressive as equally sized groups comprised of only defensive bees, and more aggressive than equally sized groups comprised only of gentle bees (Paleolog, 2009). This observation was explained by the fact that most of the attacks were carried out by the most aggressive bees. Furthermore, variation in worker aggression within a colony, but not inter-colony variation in average worker aggression, determined colony productivity in *T. longispinosus* ants (Modlmeier and Foitzik, 2011). Studies of behavioral variation among individual workers suggest that colony behavior may be affected by the distribution of worker behaviors. For example, in *T. albipennis* ants, only few individuals perform most of the work in an emigration task and most individuals perform very little of it (Dornhaus et al., 2009). Thus, it is possible that variation among colonies in emigration speed (Franks et al., 2006) will emerge from the distribution of workload within a colony and not necessarily from the average activity levels of its workers. Finally, individual variation among workers of *P. barbatus* harvester ants in interaction rate accelerates speed of information flow within a colony when compared with a situation in which all individuals have the same likelihood to interact with one another, even when the average interaction rate is the same (Pinter-Wollman et al., 2011).

1.3 Colony personality does not emerge from worker personality but from variation in local environment (external effects)

This final hypothesis suggests that colony personality results from external constrains and not from the personalities of its workers. According to this, colonies do not vary in the average or in the distribution of the worker personalities comprising them (Fig. 1C). Consistent behavioral differences among colonies result from local environments that vary consistently across time and/or situations. For example, two colonies comprised of workers with similar average activity and similar distribution of activities among workers may vary in how they respond to the environment if the nest entrance of one colony is always more shaded e.g., because it is under a tree, than the nest entrance of the other colony. Because higher temperatures elicit higher worker activity (Azcarate et al., 2007), the shaded colony will always be less responsive to changes in its environment than the colony that is in the sun.

Returning one last time to our example of foraging regulation in *P. barbatus,* this third hypothesis predicts that all workers, in all colonies respond to similar return rates. However, the environment produces variation among colonies in how they regulate foraging. For example, the nest entrance of one colony can be very narrow, allowing only 3 ants to simultaneously exit the nest, whereas the nest entrance of another colony is wide and allows 13 ants to exit simultaneously. Even if foragers return at the same rate in both colonies, theoretically resulting in similar foraging regulation, the colony with the wider entrance will be able to send out more workers per time unit than the colony with the narrow nest entrance. Thus, the colony with the wider entrance will have more flexibility in its regulation of foraging.

Environmental features indeed affect consistent individual variation among colonies. For example, *M. andrei* colonies behave consistently in both foraging and defense situations while occupying a certain nest site (Pinter-Wollman et al., 2012). Because nest structure affects how workers move (Burd et al., 2010) and interact with one another (Pinter-Wollman et al., 2011), it may determine how a colony regulates its behavior. Population density, another environmental feature, is related to the aggression level of *T. longispinosus* colonies (Modlmeier and Foitzik, 2011).

A distinction should be made here between environmental conditions that vary consistently among colonies and may determine colony personality (discussed above) and environmental changes that impact all colonies equally. When the global environment changes individual difference among colonies may persist. In fact, there may be individual variation in how colonies respond to the changes in the environment (Dingemanse et al., 2010). For example, harvester ant colonies adjust their behavior according to temperature (Cole et al., 2010) and dew point (Pinter-Wollman et al., 2012) while maintaining consistent behavioral differences among colonies.

2 How Can We Test These Hypotheses?

The first step in testing the hypotheses suggested above is identifying consistent individual variation among colonies across time and/or situations. Once colony personalities are identified, there are several ways to examine the underlying mechanisms leading to these consistent behavioral differences:

Observational studies: The behavior of colonies and their workers can be observed in the field. Natural variation among colonies in worker personality average, composition, and local environment can then be correlated with colony personality. Such studies can inform us about the effects of colony personality on their survival and reproductive success. However, cause and effect cannot be discriminated using correlational studies, which also often suffer from low statistical power and require a very large sample size.

Experimental manipulations: Artificially modifying the environment or the composition of a social insect colony can provide strong support for one hypothesis or another.

o *Colony composition:* Creating colonies, or groups, of known worker personality composition is one approach to testing the above three hypotheses. To create a group of known average worker personality or that is comprised of a known worker personality distribution, one has to assess each worker's personality. The behavior of the group as a whole can then be examined and compared under various environmental conditions. For example, one can ask whether honeybee colonies consistently vary in the amount of honey they produce because they vary in average forager efficiency (hypothesis 1), because they vary in the distribution of worker efficiency (hypothesis 2), or because of variation in their environment (hypothesis 3). Comparing the honey production of hives comprised of workers with known efficiency scores that vary in average worker efficiency, distribution of worker efficiency, or vary in their environment, will allow distinguishing between the proposed hypotheses.

One downside to this method is that individuals may change their behavior when their social setting is modified (Theraulaz et al., 1998; Robson and Traniello, 2002; Donahoe et al., 2003; O'Donnell, 2006). Furthermore, the behavior of an artificially created group might not accurately reflect the behavior of a natural colony. Still, commercial honeybee colonies are most often an aggregation of workers that were selected randomly and given an unrelated queen. Understanding how worker composition affects overall colony behavior may allow more informed bee keeping procedures that increase colony productivity (Paleolog, 2009).

o *Worker removals:* Another possible experimental manipulation is the removal of certain workers from a colony. Such removals can change both the average and the distribution of worker personalities within a colony. However, after removing workers from a colony, other individuals might take their role. Interestingly, most studies that removed workers from a colony found that 24 hours after worker removal, other individuals assume the behavioral role of the removed workers (O'Donnell, 1998; Breed et al., 2002; Gardner et al., 2007; Beverly et al., 2009). Thus, there is a short 24 hour period during which one can examine how removing certain workers affects colony behavior. Worker removals can be performed in the field (Beverly et al., 2009) under otherwise natural conditions. One caution to note when using this method is that in order to know how removals affect average and distribution of worker personality, all worker personalities in the colony must be scored, and not only the personalities of the removed workers.

o *Reducing environmental variability:* To test for effects of variation in the environment on colony behavior, colonies can be brought into the lab. One advantage of this method is that all colonies are tested in the same environment and hypotheses relating to colony composition can be tested without confounding effects of environmental heterogeneity. Other questions that can be answered by bringing colonies into controlled conditions relate to how various environmental conditions that can be manipulated in the lab, such as air temperature, affect colony personality. As with any lab study, examining colony behavior in the lab might not reflect natural colony behavior.

Computer simulations: To test whether worker composition may affect colony personality, one can use computer simulations. Such simulations will provide further information on the feasibility of the scenarios described above. The model input parameters can describe worker personalities (e.g., various behaviors that are correlated and all indicate persistence in performing a task) and the model output will be some colony level behavior in many situations (e.g., a principle component that aggregates speed of finding and depleting a food source, and speed of response to an intruder to the nest). One can then vary worker composition (average or variance of worker personalities) and test how different compositions affects the model output i.e., colony personality. Such simulations can be used to determine the effect size and sample size for detecting differences among colonies in field studies. For example, if variation among simulated colonies can be detected only when the differences among workers are greater than those observed in real populations, it is unlikely that variation among workers will determine consistent variation among colonies.

3 Mechanisms

In this paper I do not discuss in detail the possible mechanisms underlying colony composition. Little is known about what determines how each individual worker behaves and even less is known about what determines behavioral variation among workers. Thus, there is much room for studies on the mechanisms underlying behavioral variation among workers and colonies. Some mechanisms to consider include genetic, physiological, and developmental variation among workers.

Most social insect queens are multiply mated and many species have multi-queen colonies. Therefore, the queen/s produce workers that likely vary in their genetic composition which may give rise to behavioral variation among workers within a colony, as seen in bees (Latshaw and Smith, 2005). Interestingly, most queens mate only once in their lifetime and continue producing workers using sperm they collected during the mating flight. Because queens do not continue to receive sperm from males throughout their lives, the genetic composition of workers can potentially be consistent throughout a colony’s lifetime. However, recent studies show that sperm from each male within a queen’s spermatheca are clumped, resulting in temporal heterogeneity of the workers genetic composition (Wiernasz and Cole, 2010). So genetic variation among workers may result in consistent colony behavior over short time periods, on the scale of a worker’s lifespan, but the genetic composition of a colony may not necessarily be consistent throughout the queen’s lifetime.

Some species of social insects exhibit worker polymorphism, i.e. workers differ in their morphology. One classic example is the leaf cutting ant *Atta sexdens*, whose soldiers are more than an order of magnitude larger than the smallest brood-care workers (Wilson, 1980). Such variation in size determines variation in behavior, e.g., large workers are soldiers and small workers tend the brood. Such size variation is determined genetically and developmentally (Hughes et al., 2003). However, most ant species are monomorphic, i.e., do not exhibit morphological differences among workers. So physical differences are just one of potentially many manifestations of genetic or developmental variation within a colony.

The personality of a worker can be determined during its development. One extreme example comes from honey bees in which the type of food and the hormones a larva is exposed to during its development determines whether it will become a worker or a queen. Therefore, it is possible that the type of food, the temperature, and other environmental factors a worker is exposed to during its development may also determine its personality. Interestingly, this mechanism of behavioral variation among workers does not guarantee consistent average or variance of worker personalities within a colony. Colony personality may change over the course of its lifetime due to environmental changes. Thus, social insects are a useful system for further investigating some of the questions emerging from discussions on the development of personalities (Stamps and Groothuis, 2010).

Finally, the environment may also determine the distribution and average of worker personalities. For example, if temperature affects the walking speed of an ant (Azcarate et al., 2007) and certain areas in the nest are always warmer than others (maybe because they are closer to the surface) workers in those warmer areas will be more active than workers in cooler places of the nest. In addition, the environment may affect the cuticular hydrocarbon composition of ants while they are outside the nest (Wagner et al., 2001). Such chemical changes will alter the signals other ants receive from the returning ants and so the number of ants outside the nest may change the distribution of worker personalities within a colony. Such environmental effects on worker behavior link the third hypothesis with the first two. For example, if environmental conditions promote high variability in colony personality within one colony but low variance in another colony, and these two colonies exhibit different personalities, it would be difficult to determine whether these differences arise from the environmental conditions or from the degree of variation among workers.

4 We Live in a Complex World

Nature is more complex than the three scenarios I presented in this paper. Most likely, consistent behavioral variation among colonies emerges from more than one of the processes described above. Colonies likely vary in both average and distribution of worker personality and in the environmental conditions they experience.

Some behaviors may be additive and others non-additive. For example, Paleolog (2009) found that aggressive group behavior is non-additive, i.e., having only few defensive bees in the group can cause a group to be aggressive. However, colony hygiene was additive, i.e., the number of brood cells removed was directly related to the number of hygienic bees in a group.

Colonies may vary in worker personality but this may not be reflected in variation among colonies. For example, when swarming honeybee colonies choose a new nest site, colonies vary in how many workers scout for a new nest and in the number of signals performed by workers. However, when tested simultaneously, colonies do not significantly differ in how fast they chose which nest to move into (Wray and Seeley, 2011). Instead, decision speed varied among trials, and so did weather conditions, such that when temperatures were low, decision times were longer for all colonies. So variation among colonies is not always a result of variation in worker composition, environmental factors can level the playing field for all colonies, removing effects of behavioral variation at the worker level.

Furthermore, populations may vary in the predominant mechanism underlying colony personality. For example, colony personality of a population that lives in a highly heterogeneous environment may be mostly determined by local environmental differences among colonies, whereas a population of the same species that lives in a stable, homogeneous, environment may produce consistent individual differences among colonies because of variation in colony worker composition. There are also many species of social insects and it is possible that species vary among one another in how their colony personality is determined (Pearce-Duvet et al., 2011). One of the above processes e.g., variation in average worker personality, may be more pronounced in some species than in others.

As briefly mentioned earlier, a colony's personality may change over the course of its life. Sociogenesis, how colony composition changes over time, may have great implications on colony personality. Because workers are replaced throughout a colony's lifetime, colony personalities that emerge from worker composition may change as well. Furthermore, worker composition at early stages of a colony's life may affect how it develops and what kinds of workers comprise it later on, potentially affecting how its personality develops. Our ability to examine the personality of social insects at multiple levels of individuality and over the course of a life time, both of workers and of colonies, provides a unique opportunity to glean information about the mechanisms underlying the development of animal personalities. Despite these complexities, the discrete hypotheses I suggested can help us begin investigating the mechanisms underlying social insect personalities.

5 Conclusions

The three hypotheses presented here provide a theoretical basis for future paths of investigation about how social insect colony personalities emerge from worker composition and from environmental factors. The hypotheses suggest that colonies differ consistently in: the average personality of workers comprising them; the distribution of worker personalities; or their local environment. Evidence for colony personalities is slowly accumulating and the next stage of social insect personality research is to understand how these collective behaviors emerge.

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