



Personality of ant colonies (Hymenoptera: Formicidae) – underlying mechanisms and ecological consequences

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Abstract

Consistent differences in behavior among individual animals, also known as animal personalities, are ubiquitous. In social insects, there is more than one biological scale at which individuals differ from one another in behavior: workers and colonies. In most ants, natural selection acts at the level of the colony, therefore differences in collective behavior among colonies can have important ecological and evolutionary consequences. Here, we review the recent literature on consistent individual differences among ant colonies in their collective behavior, that is, colony personality. We discuss the causes and consequences of colony personalities and highlight unanswered questions that can be examined uniquely by studying ants. We argue that ants are a distinctive study system for examining the links between the mechanisms that underlie the emergence of personality and the ecological consequences of personalities because of their ability to shape their local environment, that is, their nest. We end with an example of how the study of colony personality might be applied to identify solutions for challenges in conservation biology. Overall, the study of ant colony personality opens up new opportunities for examining the evolutionary history of animal personalities and the feedback between the underlying mechanisms and ecological consequences of animal personalities.

Key words: Collective behavior, personality, behavioral syndromes, temperament, interactions, review.

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Introduction

The study of animal personalities has become a major tenet in the field of behavioral ecology over the past two decades. Consistent differences in behavior among individuals have been referred to as behavioral types, behavioral syndromes, personalities, and temperaments (SIH & al. 2004a, b, RÉALE & al. 2007). Here, we refer to personality as differences in behavior between individuals that are consistent over time and / or across situations. These consistent differences may emerge from different physiologies and developmental environments and may lead to differences in survival and reproduction.

In social animals, individual differences in behavior can occur at multiple biological scales. Individuals within a group can differ in their behavior, and groups,

as collectives, can also differ in their behavior. Here, we use the term 'colony personality' to refer to the consistent collective behaviors of colonies over time and / or across ecological situations. This use expands the definition of SIH & al. (2004b) for unitary beings to superorganisms (HÖLLDOBLER & WILSON 2009) that work collectively towards shared goals. We use the term 'collective behavior' when we refer to a collective action of a social insect colony that is not necessarily consistent over time and / or situations. Colony personalities can emerge from interactions among group members, ontogenetic processes, ecological conditions, and other processes (PINTER-WOLLMAN 2012, BENGSTON & JANDT 2014, JANDT & al. 2014).

Social insects provide a unique system in which to examine personalities at the group level because of the multilevel organization of these societies. While individual workers can differ from one another in their behavior, be it the tasks they tend to perform, the way in which they perform their tasks, or their reproductive role in the colony (TURNER 1907, JEANNE 1988), colonies also differ in their behavior from one another (PINTER-WOLLMAN 2012). Previous reviews of personality in social insects have distinguished between group- or colony-level personality and the personality of the individual workers that compose the group (JANDT & al. 2014). Here, we focus on reviewing the literature about colony-level personalities, on which the study of ants provides unique insights and opportunities for future research. Because in most ant species workers are sterile, natural selection acts at the level of the colony. Therefore, individual differences among ant colonies provide an opportunity to examine how natural selection shapes behavioral differences among groups (JANDT & GORDON 2016). The vast number of ant species provides opportunities for evolutionary comparisons that can shed light on the causes and consequences of both individual and colony personalities, and the links between them.

Here, we review the literature on the underlying causes and consequences of colony personality. Our review is not exhaustive and it emphasizes research conducted since the time a number of major reviews on ant personalities were written (PINTER-WOLLMAN 2012, BENGSTON & JANDT 2014, JANDT & al. 2014) and links this more recent work with research conducted before those reviews were written. We begin by detailing how behavioral differences among colonies can emerge. We then discuss the ecological consequences of behavioral differences between colonies, both at the population level and across ecological communities. We follow with an examination of the links between causes and consequences of colony personality by highlighting the ability of ants to construct their own niche through the formation of nests. The study of niche construction has broad implications for understanding the feedback between behavior and the environment (ODLING-SMEE & al. 1996, LALAND & al. 1999, DAY & al. 2003, ODLING-SMEE & al. 2013) and between the causes and consequences of animal personality. Ants provide a unique opportunity to study these links because of their ability to manipulate their environment. Following our review of the immediate causes and consequences of colony personality, we examine the evolutionary history of such behavioral differences, providing suggestions for future comparative work that capitalizes on the diversity of ant species. We end with an example of how the study of colony personality in ants can be applied to identify and control invasive species. Throughout the paper, we suggest topics for future research and highlight questions that the study of colony personality in ants is uniquely poised to address.

Underlying mechanisms: causes of colony personality

Many mechanisms underlie the emergence of consistent differences in behavior. Colony personality emerges from both the behavioral composition of its workers (PINTER-WOLLMAN 2012) and from the interaction patterns of these workers that produce collective behaviors (GORDON 2010). By affecting the ways in which workers interact with one another, ecological conditions can shape the behavioral rules that drive colony personality at different timescales (GORDON 2019). To explain why consistent differences in behavior among individuals exist, researchers have modeled physiological and environmental effects on behavior (SIH & al. 2015). Ants are an excellent study system to test these models because they inhabit a large range of environments, providing opportunities to compare the drivers of personality across different ecological conditions.

Group composition: Collective behaviors emerge from the behavior of the individual workers that make up the colony. Workers in a colony differ in their behavior (CHAPMAN & al. 2011), in their rate of interactions with nestmates (PINTER-WOLLMAN & al. 2011), in their morphology (OSTER & WILSON 1978), as well as in other traits. These differences can be driven by diverse genotypes (JULIAN & FEWELL 2004, WADDINGTON & al. 2010, EYER & al. 2013), differential gene expression (PAGE & al. 2018), worker age (TSCHINKEL 2004, WITTE & al. 2010), worker experience (LANGRIDGE & al. 2008), and various developmental processes (WEIDENMÜLLER & al. 2009, BENGSTON & JANDT 2014). Differences in group composition can explain differences in colony behaviors because colonies may differ in the mean and / or distribution of the types of workers that comprise them, leading to different collective outcomes (PINTER-WOLLMAN 2012). The ways in which differences among colonies in behavior might emerge from differences between individual workers in behavior have been reviewed by PINTER-WOLLMAN (2012), JANDT & al. (2014), and JANDT & GORDON (2016). Recent empirical studies on the topic have found that the exploratory behavior of *Formica fusca* workers predicts the rate at which a group transports brood (CARERE & al. 2018); the average aggression of *Linepithema humile* workers determines the response of a group to heterospecific competitors (NEUMANN & PINTER-WOLLMAN 2019); and the average exploration of *L. humile* workers explains collective nest selection (HUI & PINTER-WOLLMAN 2014). Alternatively, extreme behaviors can have important effects on collective outcomes (MODLMEIER & al. 2014). For example, nests constructed by groups of *Veromessor pergandei* composed of both large and small workers had longer and more connected tunnels than would be expected according to the additive contributions of each worker size class (KWAPICH & al. 2018). Examining how colony personalities emerge from the behaviors of the workers that compose the colony can inform the study of how consistent collective behaviors emerge in other social systems.

Interactions among workers in a colony are necessary for the emergence of collective behaviors, including the consistency of these collective behaviors (i.e., colony personality). Worker interactions regulate a variety of colony behaviors including foraging (DETRAIN & DENEUBOURG 2009), nest construction (THERAULAZ & al. 1998, 2003), nest relocation (COUZIN & FRANKS 2003, PRATT 2005a), and others. However, the way in which interactions, and potential consistency in interactions, or consistency in the mechanisms that regulate interactions, influence colony personality remains to be investigated.

Environmental effects: Colonies that experience different external conditions can exhibit different colony personalities. In *Linepithema humile*, colonies that are deprived of sucrose consistently decrease their activity and aggression compared with well-fed colonies (GROVER & al. 2007), and aphid presence decreases colony aggression (CHOE & RUST 2006). Thus, in *L. humile*, environmental conditions related to nutrition are associated with consistent differences in colony behaviors, specifically aggression and activity. Colonies that experience different environmental conditions can also exhibit different colony personalities through changes in their relative investment of worker production. For example, in *Pheidole pallidula*, colonies that sense the presence of other colonies increase their relative investment in soldier production, presumably to account for the increased likelihood of competition (PASSERA & al. 1996) and thus may exhibit different personalities from colonies that do not produce extra soldiers. The social environment can have a direct effect on colony behaviors; for example, *Temnothorax longispinosus* host colonies behave more aggressively towards their parasitic competitor *Protomognathus americanus* (now *Temnothorax americanus*, see WARD & al. 2015) compared with a non-parasitic competitor (PAMMINGER & al. 2011). Finally, colonies can differ in how they respond to similar environmental conditions and exhibit different reaction norms (DINGEMANSE & al. 2010). For example, colonies of the harvester ant *Pogonomyrmex barbatus* differ in how they regulate foraging activity in response to temperature and humidity (GORDON & al. 2011) and these differences can emerge from different gene regulation in worker brains (FRIEDMAN & al. 2018).

Alternatively, in some cases, colonies exhibit consistent differences in behavior but have similar responses to changes in the environment. For example, colonies of *Veromessor andrei* consistently differ in their responsiveness and speed across both foraging and disturbance situations. However, all colonies increase their foraging speed during dry conditions, regardless of how much they differ from one another in foraging behavior (PINTER-WOLLMAN & al. 2012). Likewise, colonies of the acorn ant *Temnothorax curvispinosus* all show similar increases in foraging rate when temperatures increase, despite differences among colonies in foraging rates in cold temperatures (MACLEAN & al. 2017). It would be interesting to determine if certain environmental features are always more likely to drive similarities or differences among colony personalities.

Future directions: The diversity of ant behaviors presents an opportunity to compare regulatory mechanisms across species that have different natural histories (GORDON 2019). We propose that comparing the mechanisms that underlie the emergence of collective behavior among colonies and species that occupy different environments can shed light on how colony personalities emerge. Such comparative studies may reveal particular environmental conditions or mechanisms of behavioral regulation (or combinations of the two) that are associated with the evolution and maintenance of personality.

Ecological consequences of colony personality

Consistent differences in behavior among individuals may influence how they respond to abiotic factors in the environment and how they interact with other species. Consistent behavioral differences among ant colonies may determine their ability to acclimate to changing climatic conditions and dictate how they interact with other colonies from their own species, other ant species, and the broader ecological community, including other animals and plants. The link between ecology and colony personality is bidirectional because the environment can influence colony personality (as discussed above), and colony personality can influence the ecological environment. We discuss this bidirectionality and potential ways to study it in the section 'Causes and consequences of colony personality are intertwined'. In this section, we focus on the consequences of colony personality at the population, community, and ecosystem levels to highlight the importance of studying ant colony personalities across ecological scales.

Relationship between colony personality and geographical distribution: Ant colonies can differ consistently in how they respond to the environment. Because ants occupy diverse niches over a wide geographic range, they present intriguing opportunities for studying the interplay between abiotic factors and animal personality. For example, *Temnothorax longispinosus* colonies from warm environments are more exploratory and more vigilant while foraging and less aggressive than colonies from cold sites (SEGEV & al. 2017). In a closely related species, *Temnothorax rugatulus*, colonies in lower latitudes – where the climate is warm – exhibit lower levels of aggression compared with colonies from cold sites. However, in contrast with *T. longispinosus*, colonies of *T. rugatulus* from warm sites have high foraging activity along short distances (BENGSTON & DORNHAUS 2014). These examples suggest that the relationship between colony personality and climate can differ between closely related species. Thus, ants provide a unique opportunity for comparing within and across species how colony personalities facilitate acclimation to abiotic conditions.

Relationship between colony personality and ecological interactions: Consistent differences in behavior may drive the outcomes of direct or indirect intra- and interspecific competition. Furthermore, ant colony personality may shape the biotic environment at the

community level due to the wide range of mutualistic and antagonistic interactions that ants have with other species.

Population level – intraspecific interactions. Colony personality can shape intraspecific interactions when competing over resources, such as territory and food. The ability to acquire and defend a nest can influence population density, leading to both direct and indirect competitive interactions among colonies. In *Temnothorax longispinosus*, colonies made up of mostly aggressive workers are better at defending their nest than colonies of the same size that consist of mostly non-aggressive individuals (MODLMEIER & al. 2014). Furthermore, intraspecific competition can change colony behavior. *Temnothorax longispinosus* colonies that interact with a conspecific competitor increase their exploration of a novel environment (MODLMEIER & al. 2012). Similarly, *Linepithema humile* colonies that regularly encounter other colonies are more aggressive than isolated colonies (THOMAS & al. 2005). Future work could untangle the relationship between the causes and consequences of population density on colony personality.

Colony personality can influence foraging strategies, which may have consequences for intraspecific competition. The foraging success of *Aphaenogaster senilis* colonies increases with colony aggression and exploratory tendencies. However, increased colony aggression and exploration leads to increased worker mortality because workers will forage at temperatures that are too high for their physiology (BLIGHT & al. 2016). Thus, the colony-level advantage of aggressive-exploratory colonies (i.e., the positive relationship between foraging and colony personality) comes at a cost to the individual workers. *Solenopsis invicta* colonies exhibit consistent differences in foraging-related behaviors, including outside activity, recruitment, and exploration (BOCKOVEN & al. 2015). High activity levels are associated with slow colony growth, suggesting that consistent differences in foraging-related behaviors may have consequences for colony fitness. Further work could compare the direct competition between colonies that exhibit different foraging behaviors and different personality traits to uncover the links between colony personality, foraging strategies, and colony fitness.

Community level – interspecific interactions. Interspecific interactions, which can be mediated by personality traits, influence communities by shaping species distribution, resource availability, and ecosystem services. Competing species may be more likely to coexist if populations contain individuals with different personalities (WOLF & WEISSING 2012). Furthermore, competition may influence the adaptive value of different behaviors in different environments (WEBSTER & al. 2009). Studying the personality of ant colonies provides an opportunity to uncover the relationship between personality and interspecific competition in a diverse clade that occupies a wide range of ecosystems. Here, we discuss the effect of colony personality on interactions among ant species and interactions between ants and other organisms.

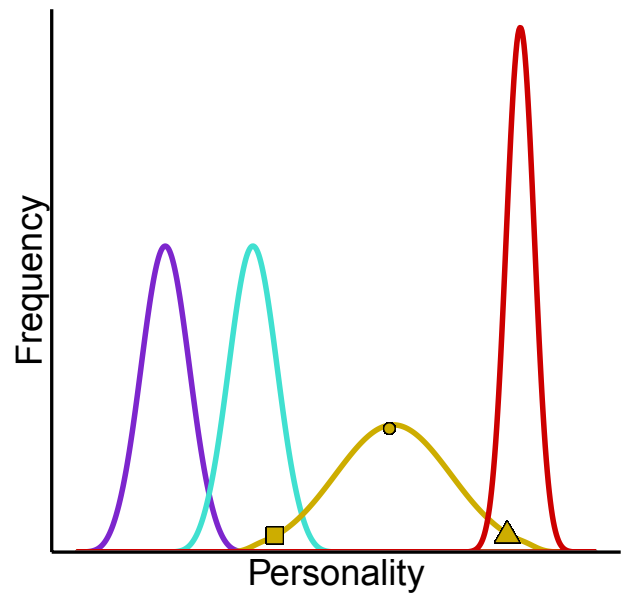


Fig. 1: Difference in colony personality within and between species for contemporaneous colonies. Hypothetical frequencies of a colony personality trait (e.g., collective aggression) of four ant species. Each species is depicted in a different color. Symbols on the distribution of the yellow species represent different colony personalities. The yellow species may face higher levels of interspecific competition than the other species because colony personalities of this species overlap with colony personalities from other species (e.g., colony personalities represented by the square and triangle). However, the yellow species may be able to withstand competition because it occupies a wider range of colony personalities than the other species, such as the red one, which has a very narrow range of colony personalities. For example, colonies with the square or circle personalities might be the most successful when the yellow and red species are competing. Colonies with personalities represented by the triangle or circle would fare better when competing with the purple and teal species. If all species are present, it is possible that over time, competition will narrow the colony personality distribution of the yellow species, leading to an increase in the number of colonies exhibiting the circle personality and eliminating those with the square or triangle colony personalities. See Figure 2 for detailed hypotheses regarding changes in the frequency of colony personalities over time.

The distribution of colony personalities within a species can influence competitive interactions, just as the distributions of other attributes shape interspecific interactions and lead to niche partitioning (HAIRSTON & al. 1960, CONNELL & ORIAS 1964). Ant species can differ in their ability to compete over and defend food and shelter (BUCZKOWSKI & BENNETT 2008, VONSHAK & al. 2012). However, the effect of colony personality on interactions among different ant species has not been explored extensively. Differences in competitive ability among colonies within a species may lead to different competitive outcomes when colonies in the extremes of the behavioral distribution of two species interact compared with interactions between colonies that

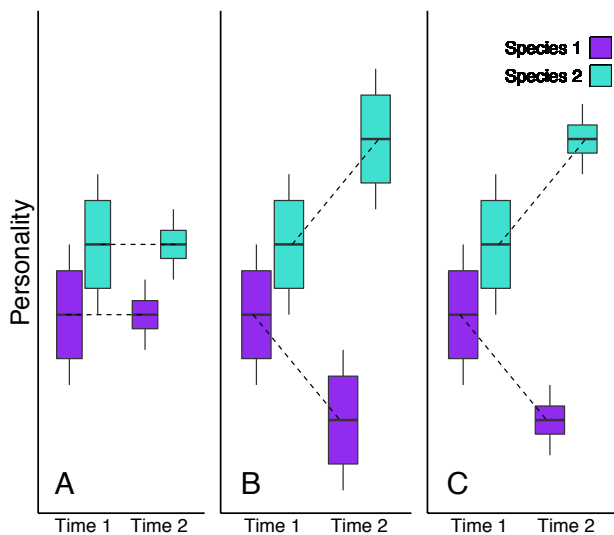


Fig. 2: Changes over time in the colony personality distribution of competing species. Three hypothetical scenarios of changes in the distributions of colony personalities when two sympatric species interact (Species 1 and 2). Each species is represented by a different color and each panel shows the potential change in colony personality distribution over time. At Time 1, the two species have similar distributions of colony personalities with some overlap (see distributions of the purple and teal species in Fig. 1). If we assume that colonies with similar personalities from different species compete with each other, we might expect that over time there will be a change in the distribution but not in the mean of colony personalities (A) or a change in the mean but not in the distribution (B). These two outcomes are not mutually exclusive and both the mean and distribution of colony personalities can change over time (C). Differences between the species at Time 2 might be smaller empirically, and are intentionally exaggerated in this hypothetical scenario to emphasize the divergence of colony personality distributions.

are close to the mean of each species (Fig. 1). Furthermore, it is possible that species with a greater diversity of colony personalities will be more successful than species with a narrower colony personality repertoire because they will be able to occupy a larger ecological niche or exhibit more strategies for competition (Fig. 1). We suggest that investigating the effects of colony personality on interspecific interactions can result in important insights about the composition of ant communities in different regions.

Further work could identify how the distribution of colony personalities of one species influences the distribution of colony personalities of a heterospecific competitor over time (Fig. 2). Colonies of *Camponotus rufipes* that overlap with a heterospecific competitor *Camponotus sericeiventris* exhibit higher levels of aggression than colonies in areas without *C. sericeiventris* (see ESPÍRITO SANTO & al. 2012). Furthermore, differences in colony personality drive coexistence between colonies of *Messor arenarius* and *Messor ebeninus*. *Messor arenarius* colonies exhibit a large range of colony personalities (similar to the yellow species in Fig. 1), compared with the narrower range of

colony personalities exhibited by *M. ebeninus* (similar to the red species in Fig. 1) (SAAR & al. 2018). Uncovering the bidirectional relationship between interspecific interactions and the distribution of colony personalities within a species addresses both the causes and consequences of colony-level personality.

Social parasitism provides a fruitful opportunity for examining the effects of colony personality on interspecific interactions. Social parasitism occurs when one ant species relies on a host species for some service, such as brood care, food, or defense (BUSCHINGER 2009, DE LA MORA & al. 2020). The personalities of both host and parasite colonies may influence the interspecific relationship and the coevolutionary arms race between the species. For example, host colonies of *Temnothorax longispinosus* increase their aggression when exposed to the parasitic *Protomognathus americanus* (see PAMMINGER & al. 2011). Colonies that exhibit high levels of aggression lose fewer brood to parasitizing colonies than colonies that exhibit low aggression, suggesting that colony personality may influence the fitness of the hosts (KLEEBERG & al. 2014). Interestingly, the rearing conditions of the host species can further influence colony personalities. In another study of *T. longispinosus* and *P. americanus*, host colonies raised by parasitic workers were faster at finding nest sites than host colonies raised by their own workers (KEISER & al. 2015). The study of colony personality can aid in understanding the evolutionary dynamics of parasite-host relationships by focusing on the costs and benefits to both host and parasite colonies that differ in their personalities. Furthermore, comparing the personalities of host colonies in ranges where social parasites have not spread with the personalities of parasitized colonies could address hypotheses about the role of social parasitism in the development of colony personality in host species.

Interspecific interactions between ants and other organisms, which shape the structure of ecological communities, can be influenced by the personalities of ant colonies. Ants can act as mutualists or parasites of plants, and colony personality may influence these ant-plant interactions. The personality of predatory species can change the community structure of prey species (WOLF & WEISSING 2012). Furthermore, a variety of parasitic microorganisms infect ants, and these associations may interact with colony personality.

Ant-plant interactions may be shaped by colony personality. For example, colony personality can influence the fitness of host plants. Highly aggressive *Azteca* colonies defend their host plants from herbivores (PRINGLE & al. 2011, MARTING & al. 2018). However, colony aggression can deter pollinators from their host plants, as happens to plants that host aggressive *Solenopsis xyloni* colonies (NESS 2006). Future work can capitalize on systems of facultative ant-plant mutualisms (APPLE & FEENER 2001, RUDGERS 2004) by comparing the personalities of colonies which live on plants with those that do not, to determine if mutualist colonies are, for example, bolder or more aggressive than colonies without a host plant.

Personality influences predator-prey interactions in a number of taxa, including birds (QUINN & al. 2012), fish (JONES & GODIN 2010), and mammals (MELLA & al. 2015). However, these interactions have received less attention in studies of social insects. Colony personality may influence colony defense from predators. Highly aggressive colonies of the harvester ant *Pogonomyrmex occidentalis* are less likely than low-aggression colonies to have predators damage their nests (WIERNASZ & al. 2014). It would be interesting to determine if trade-offs with other colony functions, such as brood care or foraging, lead low-aggression colonies to be more successful than aggressive colonies in areas with low predation rates.

Harmful microorganisms are key players in ecological systems, and their interactions, with ants may be impacted by colony personality. Small colonies of *Myrmica rubra* exhibit distinct hygienic behavior that is not seen in large colonies. When infected with a pathogen, these small colonies remove brood from the nest, sanitize the interior, and then move brood back into the nest (LECLERC & DETRAIN 2018). In *Temnothorax nylanderi*, colonies differ in the rate at which they remove infected corpses from nests (SCHARF & al. 2012). Thus, it is possible that colonies with different personality traits that are related to hygienic behavior differ in their spread of pathogens throughout the colony.

Future directions: The study of ant colony personality can advance our understanding of trophic interactions that form food webs. Because colony personalities can influence foraging strategies and predator-prey dynamics, and ant species occupy a wide range of trophic levels, colony personality could have cascading effects across food webs (KALINKAT 2014). For example, aggressive *Linepithema humile* colonies displace *Pogonomyrmex* and *Veromessor* harvester ant species, negatively impacting horned lizards that prey upon these harvester ants (SUAREZ & al. 2000). Army ants are interesting species for future studies on food webs and colony personality. For example, colonies of the army ant *Eciton burchellii* can consume tens of thousands of prey items, from a variety of species, in a single day (FRANKS & FLETCHER 1983). Thus, if there are consistent differences among colonies in their foraging behavior, they may also differ in their effects on the environment, and the distribution of colony personalities could influence the entire ecological community.

Ecological succession plays an important role in community assembly. However, despite the importance of animal personality in determining the outcomes of species interactions, few studies have considered the role of personality in ecological succession. For example, it is possible that certain personality traits fare better at different stages of succession. One might expect colonies with high levels of exploration to establish early and less exploratory colonies to settle later (FELLERS 1987, FOGARTY & al. 2011). CHAPPLE & al. (2012) provide a framework for examining the effect of personality on biological invasions, which might be applied to the study of ecological succession more broadly. Future studies could compare the person-

ality of early and late settling colonies following a major disturbance.

Changes to the environment and changes in behavior can occur at different timescales. These temporal differences can lead to a time lag between environmental changes and behavioral responses. For example, if an environmental change is rapid (e.g., a severe storm), behavioral rigidity associated with personality might not allow animals to respond to the environmental change. Colony personalities that rely on the exchange of information about the environment among workers that are spread out in space (e.g., during foraging or nest relocation) may be especially impacted by the time lag between changes in the environment and changes to colony personality. Colonies of the harvester ant *Pogonomyrmex barbatus* differ in how they regulate their foraging behavior in response to weather conditions, and these differences are heritable (GORDON 2013). Because of the long generation time of harvester ants, population-level changes to heritable colony-specific foraging strategies might take longer than changes to the weather caused by human induced climate change. Timescale differences between behavioral and environmental changes are pertinent when examining changes to nest structure, which we discuss in detail in the following section.

Causes and consequences of colony personality are intertwined

The causes and consequences of animal personality are intertwined. Ants provide a unique opportunity for examining the connections between causes and consequences of personality because many ant species shape their own niche by constructing nests or relocating between nest sites. Colony personality can impact the structures that ants occupy (e.g., through the excavation of a nest or through the decision about which nest to move into). Furthermore, nest structures can shape colony behavior because of the physical constraints that nests impose on worker interactions (PINTER-WOLLMAN 2015b, PINTER-WOLLMAN & al. 2017, 2018). Nests are diverse in structure (TSCHINKEL 2015), ranging in size from the inside of an acorn (VAROUDIS & al. 2018) to thousands of connected chambers up to seven meters deep (MOREIRA & al. 2004). The large diversity of nest structures can facilitate exploration of the relationship between colony personality and constructed niches across different ecological contexts and evolutionary histories.

Nest construction and excavation: Colonies differ in the nests they build and live in. Casts and reconstructions of nests from different colonies of the same species have different numbers of chambers (TSCHINKEL 2004, 2005, VERZA & al. 2007, GUIMARÃES & al. 2018), reach different depths (KLEINEIDAM & ROCES 2000, TSCHINKEL 2004, 2005, GUIMARÃES & al. 2018), and differ in the connectivity of the chambers (PINTER-WOLLMAN 2015a). Colonies can differ in the number of nests they occupy, as seen in the facultatively polydomous *Formica rufa* see (ELLIS & ROBINSON 2014). Among colonies, differences in

nest structure can be consistent over time. For example, when colonies of *Temnothorax rugatulus* were forced to construct a new nest four times over 12 days, some colonies tended to build wide walls while others built thin walls (DIRIENZO & DORNHAUS 2017).

The differences among colonies in nest structure could emerge from differences in how nests are constructed. The process of nest construction is driven by individual-based local rules including stigmergy and the use of local templates (THERAULAZ & al. 1998, 2003, THERAULAZ 2014, KHUONG & al. 2016, BRUCE & al. 2019, INVERNIZZI & RUXTON 2019). Species differ in the cues that workers follow when constructing a nest. For example, *Lasius niger* workers use feedback to regulate soil deposition and use body size as a template to determine the height and location of a chamber (KHUONG & al. 2016). Species of leaf cutter ants, such as *Acromyrmex lundii* and *Atta colombica*, cue on the density of workers to initiate digging behavior (RÖMER & ROCES 2014, BRUCE & al. 2019). Differences among colonies in the rules that workers follow when constructing nests, or differences among workers in the templates they use (e.g., due to polymorphism) can lead to differences in the structures that colonies live in (KWAPOCH & al. 2018).

The nest, as an extended phenotype, can shape the collective behavior of colonies and their personality. Nest structure can shape differences among colonies in behavior (PINTER-WOLLMAN 2015a, PINTER-WOLLMAN & al. 2017). For example, nest architecture can shape patterns of worker interactions (PINTER-WOLLMAN 2015b), which underlie collective behavior. Indeed, the foraging behavior of *Veromessor andrei* harvester ant colonies is influenced by the structure of their nests (PINTER-WOLLMAN 2015a). The collective behavior of these colonies is consistent as long as they remain in a particular nest site (and can therefore be considered a colony personality) but their behavior changes when they move to a new nest (PINTER-WOLLMAN & al. 2012). Because nests can shape colony behavior and the behavior of the colony (e.g., excavation or relocation) can shape the structure of the nest, ants provide a unique opportunity to examine feedback between animal personality and the environment.

Nest relocation: One form of niche construction is relocating into a new nest. Colonies can move regularly among a set of nests (MCGLYNN 2007), in response to a destruction of their nest (MÖGLICH 1978), to avoid interactions with conspecifics (BROWN 1999), or when scouts encounter high quality nests (DORNHAUS & al. 2004). Within and between populations, colonies can differ in how frequently they relocate among nests (PINTER-WOLLMAN & BROWN 2015). These relocations place colonies in different nest structures, which, as discussed in the previous section, can shape colony personality. In addition, colonies may differ consistently in how frequently they relocate among nests and these differences may be affected by other colony behaviors. For example, in *Temnothorax nylanderi*, there is a negative relationship between colony aggression and the likelihood to relocate into a new nest (SCHARF & al. 2012).

Studying how colonies collectively choose which nests to relocate into can uncover how different processes may lead to consistent differences in nest site preferences. For example, among-colony differences in nest preference may emerge from differences in the quorum size that colonies require to transition from tandem running to active transport, as has been studied extensively in *Temnothorax* ants (PRATT 2005a, b, PRATT & SUMPTER 2006). In *Myrmecina nipponica*, colonies use pheromone trails to navigate and recruit individuals to a new nest site until reaching a quorum threshold to start active transport of workers and brood (CRONIN 2013).

The decisions whether to relocate, and which nest site to move into, may be influenced by environmental features. These environmental effects on nest relocation can be studied by comparing colonies within and among species that occupy similar, or different, environments. For example, in populations of the harvester ant *Pogonomyrmex barbatus*, 20% of colonies attempt to relocate every year but only 10% successfully move (GORDON 1992). It would be interesting to determine what causes only half of the colonies to relocate successfully. Perhaps there are micro-climatic features or certain traits that facilitate the relocation success of some colonies but not others. In contrast with *P. barbatus*, up to 80% of colonies of the harvester ant *Veromessor andrei* relocate annually (BROWN 1999). *Veromessor andrei* live in serpentine grasslands (HOBBS 1985, BROWN 1999) which have different soils from where *P. barbatus* dig their nests. Thus, it is possible that soil structure leads to differences in relocation frequency among species and local differences in soil structure could drive differences among colonies of the same species in nest relocation behavior. Studying such environmental effects on relocation behavior can expand our understanding of the feedback between the environment and colony personality.

Future directions: The ability of ants to construct the niches they live in provides an intriguing opportunity to study the feedback between the environment and personality. Colony personality may affect how frequently colonies relocate among nests or how they construct the nests they live in. In addition, the nests that colonies construct or choose to relocate into may impact colony personality because nest structure influences worker interaction patterns (BURD & al. 2010, PINTER-WOLLMAN & al. 2013, PINTER-WOLLMAN 2015b). These interaction patterns determine collective behaviors, including the collective decision-making process during nest relocation and potentially the decisions made during nest construction. Thus, ants provide a study system in which multiple components can be manipulated to investigate the feedback between nest structure and collective behaviors and / or colony personalities, and more broadly, the built environment and collective outcomes (PINTER-WOLLMAN & al. 2018).

Differences among colonies and species in how they construct their nests or how frequently they relocate nests could emerge from differences in environmental stability. If colonies modify their behaviors in response to changes

in the environment, then we may expect colonies that live in stable environments to have different nest construction and relocation patterns than colonies that live in unstable environments. For example, in unstable environments, colonies might change the structure of their nests over time in response to changes in the environment (e.g., colonies that live in rainy environments may modify nests more frequently to repair damage caused by rains). Future research could explore how differences in the timescale over which collective behaviors change and the environment changes affect the feedback between the two and shape colony personalities. Because ants live in a range of environments that differ in stability and because they can shape their local environment, they are a powerful system in which to study the feedback between consistent differences in behavior and environmental changes, which can occur at different timescales.

Evolution of colony personality

Ants provide a unique opportunity to examine the evolutionary trajectory of animal personalities. While some theory has investigated possible explanations for how personalities have evolved (WOLF & WEISSING 2010, SIH & al. 2015), empirical evidence is still lacking. The comparative approach is one of the primary ways to study the evolution of behavior because behavior typically does not leave a fossil record (HSIEH & PLOTNICK 2020). The diversity of ants, with more than 12,000 identified species (HÖLDOBLER & WILSON 1990), can facilitate comparative investigation of the evolution of colony personality. By comparing across species that have similar or different life history traits, ecological roles, and environmental constraints, we can uncover sources of differences among colonies. When conducting comparative analyses (e.g., meta-analyses), one must consider the literature that is sampled, as some questions have received more attention than others. It is further important to be cautious when choosing which data to compare because there might be differences in how behaviors are measured and reported.

Sources of differences between colonies: Within a species, colonies may differ in the selection pressures they experience, with species that have larger distribution ranges often experiencing greater differences among colonies and species with smaller ranges potentially experiencing more uniform pressures. Species' distribution can help explain the evolution and maintenance of different colony personality types as well as the amount of behavioral diversity across individuals and populations. Depending on which colony personality is examined, it can be quantified as either a continuous or a discrete trait. Comparing the degree to which colonies differ in their personality across different species, which occupy different geographical ranges and environments, may help uncover the relationship between species distribution, evolutionary pressures, and personality. For example, one could compare differences in colony personalities among related or unrelated species that have different or similar distribution ranges.

If evolution favors a high degree of behavioral diversity in species with a large distribution range, we would expect different species that occupy large ranges to exhibit similar levels of behavioral diversity compared with species which occupy small ranges. If, however, phylogenetic similarity is a better predictor of behavioral diversity than distribution range size, we might expect closely related species to exhibit a similar degree of behavioral diversity, regardless of the geographical range and environments they each occupy. For example, *Temnothorax longispinosus* (see SEGEV & al. 2017) and *Temnothorax rugatulus* (see BENGSTON & DORNHAUS 2014) are closely related species that exhibit similar amounts of differences among colonies in personality, despite having differently sized geographic ranges. Thus, it is possible that the shared phylogenetic history of these two species provides a better explanation for their similarities in behavioral diversity than the size of their geographical range.

Comparisons among species can help determine the causes that underlie the emergence of personality and disentangle heritable components from developmental causes. In some species, personality may be driven predominantly by genetic effects, whereas in others it may emerge primarily from ontogenetic effects. Comparing species can reveal which ecological conditions might favor genetic or developmental drivers for colony personality. For example, in *Pogonomyrmex barbatus*, younger colonies are more aggressive towards conspecifics than older colonies (GORDON 1991, 1995). In contrast, *Temnothorax rugatulus* colonies do not show a relationship between age and aggression (BENGSTON & DORNHAUS 2014). Instead, colonies that grow faster and invest more in reproductives (queens and males) are more aggressive compared with colonies that grow slower and invest more in sterile workers (BENGSTON & al. 2017). Thus, the drivers and presence of consistent individual differences between colonies likely differ between these two species: In *P. barbatus*, colony aggressive behavior is plastic and changes over development, whereas in *T. rugatulus*, colony aggressive behavior is stable over a lifetime and therefore might have stronger genetic drivers than in *P. barbatus*, forming a life-long colony personality. Such comparisons among species of ants might uncover novel sources of consistent differences among colonies in behavior.

Application of the study of ant colony personalities

Colony personality can mediate the ways in which ants interact with their environment, as detailed in previous sections. The invasion by ants into novel ecosystems represents an important link between colony behavior and the environment (MCGLYNN 1999, TSUTSUI & SUAREZ 2003, WEIS & SOL 2016). Invasive ants are a concern across ecosystems globally because they displace native species and disrupt ecological communities (MCGLYNN 1999, HOLWAY & al. 2002, BOS & al. 2008). Although many ant species have the opportunity to invade new habitats, only a fraction of them successfully establish and persist (SUAREZ &

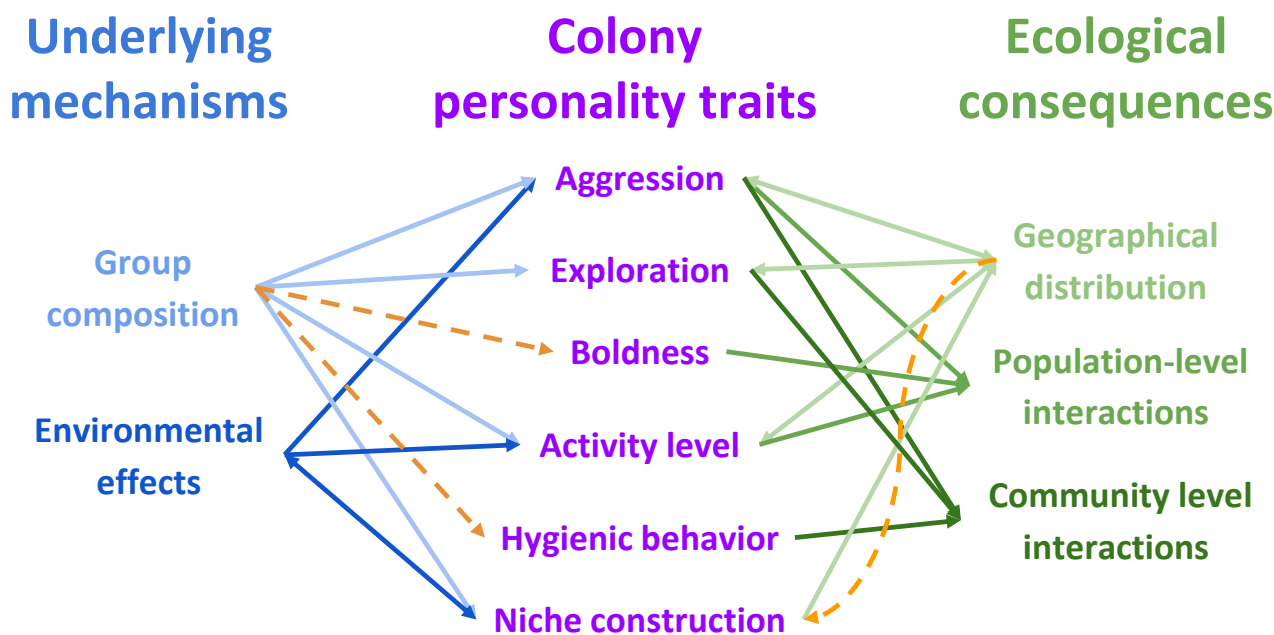


Fig. 3: Summary of the relationships between the causes and consequences of colony personality that we identified in our review. Solid arrows are links that we discussed in the review. Dashed orange lines are a few of the many relationships we propose would be interesting topics for future research.

al. 2005). Ten genera and at least 150 species of ants have invaded native ecosystems (HOLWAY & al. 2002, CREMER & al. 2008), making ants a good system for the study of personality and conservation biology.

Characteristics of invasive species: Invasive ant species may share colony-level traits, including certain collective behaviors that allow them to successfully expand into new ranges. These traits include flexibility in nesting behavior and dietary requirements, polygyny (multiple queens), colony reproduction by budding, and reduced intraspecific aggression (MCGLYNN 1999, HOLWAY & al. 2002, TSUTSUI & SUAREZ 2003). Furthermore, invasive populations express different collective behaviors from those observed in native populations (SUAREZ & al. 1999, HOLWAY & al. 2002). For example, in Europe, invasive colonies of *Linepithema humile* explore novel environments and detect food resources more quickly than their native counterparts (BLIGHT & al. 2017). Similarly, colonies of *L. humile* in North America are more aggressive than native colonies, potentially facilitating the displacement of native ants in the invaded range (HELLER 2004). However, the mechanisms that underlie the plasticity that facilitates these behavioral differences is likely the same in introduced and native populations (FELDEN & al. 2018). Invasive colonies of *Solenopsis invicta* that are located far from the initial introduction location of the species in North America exhibit higher levels of exploration and forager recruitment than colonies near the site of introduction (BOCKOVEN 2015). While these invasive characteristics have been observed in a variety of ant species, future research may examine how features of the environment, such as food availability or

seasonality, affect colony personality, because there can be differences in the traits that characterize invasive species in non-native populations based on access to certain foods.

Colony personality and conservation biology: Ants provide an opportunity to study the effects of personality on invasion risk. While current invasion biology research has begun to uncover the impacts of invasions, how personality influences the probability of successful colonization by invasive species is not well known. The study of ant colony personality can benefit the field of conservation biology by providing information on key characteristics of invasive species. For example, *Linepithema humile* workers are attracted to water in urban areas (HOLWAY & SUAREZ 2006, FITZGERALD & al. 2012, FITZGERALD & GORDON 2012). If there are individual differences among colonies (in the native or invaded range) in their reliance on water, this information could prove useful for determining which colonies might invade arid regions and could be used for controlling or preventing invasion. By studying ant colony personality, we can construct risk assessments that will help prevent the continued spread of invasive ants. Furthermore, studying personality can help identify which species have the potential to be invasive and if any personality traits are associated with the native species that withstand invasion. Such a study could help predict which native species will be impacted the most by the introduction of an invasive species (e.g., Figs. 1 and 2).

Studies of colony personalities can improve our understanding of how personality affects the stages of an invasion – transport, introduction, establishment, and spread. Animal personality can affect introduction success

because different personality traits might have different impacts on the different stages of invasions. Furthermore, species invasion may act as a selective force in the introduced range – favoring personality traits that promote invasion success (CHAPPLE & al. 2012). Comparisons of personality traits among species or individuals that are successful at invading new habitats and those that are not, can inform conservation actions (WRIGHT & al. 2010). Understanding the dynamics of an invasion could provide researchers with insight on how invasive ants are established and during which stages of invasion they are most vulnerable to management.

Conclusion

In our examination of the literature on ant colony personality, we identified a range of links between the causes and consequences of colony personality, as well as topics for future investigation (Fig. 3). We highlight future research efforts that could be addressed uniquely through studies on ants. The diversity of ant species opens up countless opportunities for examining the underlying causes and ecological consequences of personality at multiple scales. The diversity of ants leaves many unexplored species and ecological systems and provides ample opportunities for comparative work. Ants provide a unique system in which to study the feedback between causes and consequences of personality because of their ability to modify the environment in which they live. We believe that future work on ant colony personality will benefit the broad field of animal personality by capitalizing on the exceptional features of ants.

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References

APPLE, J. & FEENER, D. 2001: Ant visitation of extrafloral nectaries of *Passiflora*: the effects of nectary attributes and ant behavior on patterns in facultative ant-plant mutualisms. – *Oecologia* 127: 409-416.

BENGSTON, S.E. & DORNHAUS, A. 2014: Be meek or be bold? A colony-level behavioural syndrome in ants. – *Proceedings of the Royal Society B-Biological Sciences* 281: art. 20140518.

BENGSTON, S.E. & JANDT, J.M. 2014: The development of collective personality: the ontogenetic drivers of behavioral variation across groups. – *Frontiers in Ecology and Evolution* 2: art. 81.

BENGSTON, S.E., SHIN, M. & DORNHAUS, A. 2017: Life-history strategy and behavioral type: risk-tolerance reflects growth rate and energy allocation in ant colonies. – *Oikos* 126: 556-564.

BLIGHT, O., JOSENS, R., BERTELSMEIER, C., ABRIL, S., BOULAY, R. & CERDÁ, X. 2017: Differences in behavioural traits among native and introduced colonies of an invasive ant. – *Biological Invasions* 19: 1389-1398.

BLIGHT, O., VILLALTA, I., CERDÁ, X. & BOULAY, R. 2016: Personality traits are associated with colony productivity in the gypsy ant *Aphaenogaster senilis*. – *Behavioral Ecology and Sociobiology* 70: 2203-2209.

BOCKOVEN, A.A. 2015: Causes and consequences of intraspecific variation in behavior of the red imported fire ant. – PhD thesis, Texas A&M University, College Station, TX, XI+125 pp.

BOCKOVEN, A.A., WILDER, S.M. & EUBANKS, M.D. 2015: Intraspecific variation among social insect colonies: persistent regional and colony-level differences in fire ant foraging behavior. – *Public Library of Science One* 10: art. e0133868.

BOS, M.M., TYLIANAKIS, J.M., STEFFAN-DEWENTER, I. & TSCHARNTKE, T. 2008: The invasive yellow crazy ant and the decline of forest ant diversity in Indonesian cacao agroforests. – *Biological Invasions* 10: 1399-1409.

BROWN, M.J.F. 1999: Nest relocation and encounters between colonies of the seed-harvesting ant *Messor andrei*. – *Insectes Sociaux* 46: 66-70.

BRUCE, A.I., PÉREZ-ESCUADERO, A., CZACZKES, T.J. & BURD, M. 2019: The digging dynamics of ant tunnels: movement, encounters, and nest space. – *Insectes Sociaux* 66: 119-127.

BUCZKOWSKI, G. & BENNETT, G.W. 2008: Aggressive interactions between the introduced Argentine ant, *Linepithema humile* and the native odorous house ant, *Tapinoma sessile*. – *Biological Invasions* 10: 1001-1011.

BURD, M., SHIWAKOTI, N., SARVI, M. & ROSE, G. 2010: Nest architecture and traffic flow: large potential effects from small structural features. – *Ecological Entomology* 35: 464-468.

BUSCHINGER, A. 2009: Social parasitism among ants: a review (Hymenoptera: Formicidae). – *Myrmecological News* 12: 219-235.

CARERE, C., AUDEBRAND, C., RÖDEL, H.G. & D'ETTORRE, P. 2018: Individual behavioural type and group performance in *Formica fusca* ants. – *Behavioural Processes* 157: 402-407.

CHAPMAN, B.B., THAIN, H., COUGHLIN, J. & HUGHES, W.O.H. 2011: Behavioural syndromes at multiple scales in *Myrmica* ants. – *Animal Behaviour* 82: 391-397.

CHAPPLE, D.G., SIMMONDS, S.M. & WONG, B.B.M. 2012: Can behavioral and personality traits influence the success of unintentional species introductions? – *Trends in Ecology & Evolution* 27: 57-64.

CHOE, D.-H. & RUST, M.K. 2006: Homopteran chemical signatures reduce aggression of tending ants. – *Chemoecology* 16: 175-178.

CONNELL, J.H. & ORIAS, E. 1964: The ecological regulation of species diversity. – *The American Naturalist* 98: 399-414.

COUZIN, I.D. & FRANKS, N.R. 2003: Self-organized lane formation and optimized traffic flow in army ants. – *Proceedings of the Royal Society B-Biological Sciences* 270: 139-146.

CREMER, S., UGELVIG, L.V., DRIJFHOUT, F.P., SCHLICK-STEINER, B.C., STEINER, F.M., SEIFERT, B., HUGHES, D.P., SCHULZ, A., PETERSEN, K.S., KONRAD, H., STAUFFER, C., KIRAN, K., ESPADALER, X., D'ETTORRE, P., AKTAÇ, N., EILENBERG, J., JONES, G.R., NASH, D.R., PEDERSEN, J.S. & BOOMSMA, J.J. 2008: The evolution of invasiveness in garden ants. – *Public Library of Science One* 3: art. e3838.

CRONIN, A.L. 2013: Synergy between pheromone trails and quorum thresholds underlies consensus decisions in the ant *Myrmecina nipponica*. – *Behavioral Ecology and Sociobiology* 67: 1643-1651.

DAY, R.L., LALAND, K.N. & ODLING-SMEE, F.J. 2003: Rethinking adaptation: the niche-construction perspective. – *Perspectives in Biology and Medicine* 46: 80-95.

DE LA MORA, A., SANKOVITZ, M. & PURCELL, J. 2020: Ants (Hymenoptera: Formicidae) as host and intruder: recent advances and future directions in the study of exploitative strategies. – *Myrmecological News* 30: 53-71.

- DETRAIN, C. & DENEUBOURG, J.-L. 2009: Social cues and adaptive foraging strategies in ants. In: JARAU, S. & HRNCIR, M. (Eds.): Food exploitation by social insects. – CRC Press, Boca Raton, FL, pp. 29-54.
- DINGEMANSE, N.J., KAZEM, A.J.N., RÉALE, D. & WRIGHT, J. 2010: Behavioural reaction norms: animal personality meets individual plasticity. – Trends in Ecology & Evolution 25: 81-89.
- DIRIENZO, N. & DORNHAUS, A. 2017: *Temnothorax rugatulus* ant colonies consistently vary in nest structure across time and context. – Public Library of Science One 12: art. e0177598.
- DORNHAUS, A., FRANKS, N.R., HAWKINS, R.M. & SHERE, H.N.S. 2004: Ants move to improve: colonies of *Leptothorax albi-pennis* emigrate whenever they find a superior nest site. – Animal Behaviour 67: 959-963.
- ELLIS, S. & ROBINSON, E.J.H. 2014: Polydomy in red wood ants. – Insectes Sociaux 61: 111-122.
- ESPÍRITO SANTO, N.B. DO, RIBEIRO, S.P. & SANTOS LOPES, J.F. 2012: Evidence of competition between two canopy ant species: is aggressive behavior innate or shaped by a competitive environment? – Psyche 2012: art. 609106.
- EYER, P.-A., FREYER, J. & ARON, S. 2013: Genetic polyethism in the polyandrous desert ant *Cataglyphis cursor*. – Behavioral Ecology 24: 144-151.
- FELDEN, A., PARIS, C.I., CHAPPLE, D.G., HAYWOOD, J., SUAREZ, A.V., TSUTSUI, N.D., LESTER, P.J. & GRUBER, M.A. 2018: Behavioural variation and plasticity along an invasive ant introduction pathway. – Journal of Animal Ecology 87: 1653-1666.
- FELLERS, J.H. 1987: Interference and exploitation in a guild of woodland ants. – Ecology 68: 1466-1478.
- FITZGERALD, K. & GORDON, D.M. 2012: Effects of vegetation cover, presence of a native ant species, and human disturbance on colonization by Argentine ants. – Conservation Biology 26: 525-538.
- FITZGERALD, K., HELLER, N. & GORDON, D.M. 2012: Modeling the spread of the Argentine ant into natural areas: habitat suitability and spread from neighboring sites. – Ecological Modelling 247: 262-272.
- FOGARTY, S., COTE, J. & SIH, A. 2011: Social personality polymorphism and the spread of invasive species: a model. – The American Naturalist 177: 273-287.
- FRANKS, N.R. & FLETCHER, C.R. 1983: Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado Island, Panama. – Behavioral Ecology and Sociobiology 12: 261-270.
- FRIEDMAN, D.A., PILKO, A., SKOWRONSKA-KRAWCZYK, D., KRASINSKA, K., PARKER, J.W., HIRSH, J. & GORDON, D.M. 2018: The role of dopamine in the collective regulation of foraging in harvester ants. – iScience 8: 283-294.
- GORDON, D.M. 1991: Behavioral flexibility and the foraging ecology of seed-eating ants. – The American Naturalist 138: 379-411.
- GORDON, D.M. 1992: Nest relocation in harvester ants. – Annals of the Entomological Society of America 85: 44-47.
- GORDON, D.M. 1995: The expandable network of ant exploration. – Animal Behaviour 50: 995-1007.
- GORDON, D.M. 2010: Ant encounters: interaction networks and colony behavior. – Princeton University Press, Princeton, NJ, 184 pp.
- GORDON, D.M. 2013: The rewards of restraint in the collective regulation of foraging by harvester ant colonies. – Nature 498: 91-93.
- GORDON, D.M. 2019: The ecology of collective behavior in ants. – Annual Review of Entomology 64: 35-50.
- GORDON, D.M., GUETZ, A., GREENE, M.J. & HOLMES, S. 2011: Colony variation in the collective regulation of foraging by harvester ants. – Behavioral Ecology 22: 429-435.
- GROVER, C.D., KAY, A.D., MONSON, J.A., MARSH, T.C. & HOLWAY, D.A. 2007: Linking nutrition and behavioural dominance: carbohydrate scarcity limits aggression and activity in Argentine ants. – Proceedings of the Royal Society B-Biological Sciences 274: 2951-2957.
- GUIMARÃES, I. DE C., PEREIRA, M.C., BATISTA, N.R., RODRIGUES, C.A.P. & ANTONIALLI, W.F. 2018: The complex nest architecture of the Ponerinae ant *Odontomachus chelifer*. – Public Library of Science One 13: art. e0189896.
- HAIRSTON, N.G., SMITH, F.E. & SLOBODKIN, L.B. 1960: Community structure, population control, and competition. – The American Naturalist 94: 421-425.
- HELLER, N.E. 2004: Colony structure in introduced and native populations of the invasive Argentine ant, *Linepithema humile*. – Insectes Sociaux 51: 378-386.
- HOBBS, R.J. 1985: Harvester ant foraging and plant species distribution in annual grassland. – Oecologia 67: 519-523.
- HÖLLDOBLER, B. & WILSON, E.O. 1990: The ants. – Harvard University Press, Cambridge, MA, 784 pp.
- HÖLLDOBLER, B. & WILSON, E.O. 2009: The superorganism: the beauty, elegance, and strangeness of insect societies. – W.W. Norton & Company, New York, NY, 544 pp.
- HOLWAY, D.A., LACH, L., SUAREZ, A.V., TSUTSUI, N.D. & CASE, T.J. 2002: The causes and consequences of ant invasions. – Annual Review of Ecology and Systematics 33: 181-233.
- HOLWAY, D.A. & SUAREZ, A.V. 2006: Homogenization of ant communities in mediterranean California: The effects of urbanization and invasion. – Biological Conservation 127: 319-326.
- HSIEH, S. & PLOTNICK, R.E. 2020: The representation of animal behaviour in the fossil record. – Animal Behaviour 169: 65-80.
- HUI, A. & PINTER-WOLLMAN, N. 2014: Individual variation in exploratory behaviour improves speed and accuracy of collective nest selection by Argentine ants. – Animal Behaviour 93: 261-266.
- INVERNIZZI, E. & RUXTON, G.D. 2019: Deconstructing collective building in social insects: implications for ecological adaptation and evolution. – Insectes Sociaux 66: 507-518.
- JANDT, J.M., BENGSTON, S., PINTER-WOLLMAN, N., PRUITT, J.N., RAINE, N.E., DORNHAUS, A. & SIH, A. 2014: Behavioural syndromes and social insects: personality at multiple levels. – Biological Reviews 89: 48-67.
- JANDT, J.M. & GORDON, D.M. 2016: The behavioral ecology of variation in social insects. – Current Opinion in Insect Science 15: 40-44.
- JEANNE, R.L. 1988: Interindividual behavioral variability in social insects. – CRC Press, Boca Raton, FL, 316 pp.
- JONES, K.A. & GODIN, J.-G.J. 2010: Are fast explorers slow reactors? Linking personality type and anti-predator behaviour. – Proceedings of the Royal Society B-Biological Sciences 277: 625-632.
- JULIAN, G.E. & FEWELL, J.H. 2004: Genetic variation and task specialization in the desert leaf-cutter ant, *Acromyrmex versicolor*. – Animal Behaviour 68: 1-8.
- KALINKAT, G. 2014: Bringing animal personality research into the food web arena. – Journal of Animal Ecology 83: 1245-1247.
- KEISER, C.N., WRIGHT, C.M., SINGH, N., DESHANE, J.A., MODLMEIER, A.P. & PRUITT, J.N. 2015: Cross-fostering by foreign conspecific queens and slave-making workers influences individual- and colony-level personality. – Behavioral Ecology and Sociobiology 69: 395-405.

- KHUONG, A., GAUTRAIS, J., PERNA, A., SBAÏ, C., COMBE, M., KUNTZ, P., JOST, C. & THERAULAZ, G. 2016: Stigmergic construction and topochemical information shape ant nest architecture. – *Proceedings of the National Academy of Sciences of the United States of America* 113: 1303-1308.
- KLEEBERG, I., PAMMINGER, T., JONGEPIER, E., PAPENHAGEN, M. & FOITZIK, S. 2014: Forewarned is forearmed: aggression and information use determine fitness costs of slave raids. – *Behavioral Ecology* 25: 1058-1063.
- KLEINEIDAM, C. & ROCES, F. 2000: Carbon dioxide concentrations and nest ventilation in nests of the leaf-cutting ant *Atta vollenweideri*. – *Insectes Sociaux* 47: 241-248.
- KWAPICH, C.L., VALENTINI, G. & HÖLLDOBLER, B. 2018: The non-additive effects of body size on nest architecture in a polymorphic ant. – *Philosophical Transactions of the Royal Society B-Biological Sciences* 373: art. 20170235.
- LALAND, K.N., ODLING-SMEE, F.J. & FELDMAN, M.W. 1999: Evolutionary consequences of niche construction and their implications for ecology. – *Proceedings of the National Academy of Sciences of the United States of America* 96: 10242-10247.
- LANGRIDGE, E.A., SENDOVA-FRANKS, A.B. & FRANKS, N.R. 2008: How experienced individuals contribute to an improvement in collective performance in ants. – *Behavioral Ecology and Sociobiology* 62: 447-456.
- LECLERC, J.-B. & DETRAIN, C. 2018: Impact of colony size on survival and sanitary strategies in fungus-infected ant colonies. – *Behavioral Ecology and Sociobiology* 72: art. 3.
- MACLEAN, H.J., PENICK, C.A., DUNN, R.R. & DIAMOND, S.E. 2017: Experimental winter warming modifies thermal performance and primes acorn ants for warm weather. – *Journal of Insect Physiology* 100: 77-81.
- MARTING, P.R., KALLMAN, N.M., WCISLO, W.T. & PRATT, S.C. 2018: Ant-plant sociometry in the *Azteca-Cecropia* mutualism. – *Scientific Reports* 8: 1-15.
- MCGLYNN, T.P. 1999: The worldwide transfer of ants: geographical distribution and ecological invasions. – *Journal of Biogeography* 26: 535-548.
- MCGLYNN, T.P. 2007: Serial monodomy in ants: an antipredator strategy? – *Ecological Entomology* 32: 621-626.
- MELLA, V.S., WARD, A.J., BANKS, P.B. & MCARTHUR, C. 2015: Personality affects the foraging response of a mammalian herbivore to the dual costs of food and fear. – *Oecologia* 177: 293-303.
- MODLMEIER, A.P., KEISER, C.N., SHEARER, T.A. & PRUITT, J.N. 2014: Species-specific influence of group composition on collective behaviors in ants. – *Behavioral Ecology and Sociobiology* 68: 1929-1937.
- MODLMEIER, A.P., LIEBMANN, J.E. & FOITZIK, S. 2012: Diverse societies are more productive: a lesson from ants. – *Proceedings of the Royal Society B-Biological Sciences* 279: 2142-2150.
- MÖGLICH, M. 1978: Social organization of nest emigration in *Leptothorax* (Hym., Form.). – *Insectes Sociaux* 25: 205-225.
- MOREIRA, A., FORTI, L.C., ANDRADE, A.P., BOARETTO, M.A. & LOPES, J. 2004: Nest architecture of *Atta laevigata* (F. SMITH, 1858) (Hymenoptera: Formicidae). – *Studies on Neotropical Fauna and Environment* 39: 109-116.
- NESS, J.H. 2006: A mutualism's indirect costs: the most aggressive plant bodyguards also deter pollinators. – *Oikos* 113: 506-514.
- NEUMANN, K.M. & PINTER-WOLLMAN, N. 2019: Collective responses to heterospecifics emerge from individual differences in aggression. – *Behavioral Ecology: Official Journal of the International Society for Behavioral Ecology* 30: 801-808.
- ODLING-SMEE, F.J., LALAND, K.N. & FELDMAN, M.W. 1996: Niche construction. – *The American Naturalist* 147: 641-648.
- ODLING-SMEE, J., ERWIN, D.H., PALKOVACS, E.P., FELDMAN, M.W. & LALAND, K.N. 2013: Niche construction theory: a practical guide for ecologists. – *The Quarterly Review of Biology* 88: 3-28.
- OSTER, G.F. & WILSON, E.O. 1978: *Caste and ecology in the social insects*. – Princeton University Press, Princeton, NJ, 372 pp.
- PAGE, H., SWEENEY, A., PILKO, A. & PINTER-WOLLMAN, N. 2018: Underlying mechanisms and ecological context of variation in exploratory behavior of the Argentine ant, *Linepithema humile*. – *Journal of Experimental Biology* 221: art. jeb188722.
- PAMMINGER, T., SCHARF, I., PENNING, P.S. & FOITZIK, S. 2011: Increased host aggression as an induced defense against slave-making ants. – *Behavioral Ecology* 22: 255-260.
- PASSERA, L., RONCIN, E., KAUFMANN, B. & KELLER, L. 1996: Increased soldier production in ant colonies exposed to intraspecific competition. – *Nature* 379: 630-631.
- PINTER-WOLLMAN, N. 2012: Personality in social insects: How does worker personality determine colony personality? – *Current Zoology* 58: 580-588.
- PINTER-WOLLMAN, N. 2015a: Nest architecture shapes the collective behaviour of harvester ants. – *Biology Letters* 11: art. 20150695.
- PINTER-WOLLMAN, N. 2015b: Persistent variation in spatial behavior affects the structure and function of interaction networks. – *Current Zoology* 61: 98-106.
- PINTER-WOLLMAN, N., BALA, A., MERRELL, A., QUEIROLO, J., STUMPE, M.C., HOLMES, S. & GORDON, D.M. 2013: Harvester ants use interactions to regulate forager activation and availability. – *Animal behaviour* 86: 197-207.
- PINTER-WOLLMAN, N. & BROWN, M.J.F. 2015: Variation in nest relocation of harvester ants is affected by population density and food abundance. – *Behavioral Ecology* 26: 1569-1576.
- PINTER-WOLLMAN, N., FIORE, S.M. & THERAULAZ, G. 2017: The impact of architecture on collective behaviour. – *Nature Ecology and Evolution* 1: 1-2.
- PINTER-WOLLMAN, N., GORDON, D.M. & HOLMES, S. 2012: Nest site and weather affect the personality of harvester ant colonies. – *Behavioral Ecology* 23: 1022-1029.
- PINTER-WOLLMAN, N., PENN, A., THERAULAZ, G. & FIORE, S.M. 2018: Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour. – *Philosophical Transactions of the Royal Society B-Biological Sciences* 373: 20170232.
- PINTER-WOLLMAN, N., WOLLMAN, R., GUETZ, A., HOLMES, S. & GORDON, D.M. 2011: The effect of individual variation on the structure and function of interaction networks in harvester ants. – *Journal of the Royal Society Interface* 8: 1562-1573.
- PRATT, S.C. 2005a: Behavioral mechanisms of collective nest-site choice by the ant *Temnothorax curvispinosus*. – *Insectes Sociaux* 52: 383-392.
- PRATT, S.C. 2005b: Quorum sensing by encounter rates in the ant *Temnothorax albipennis*. – *Behavioral Ecology* 16: 488-496.
- PRATT, S.C. & SUMPTER, D.J.T. 2006: A tunable algorithm for collective decision-making. – *Proceedings of the National Academy of Sciences of the United States of America* 103: 15906-15910.
- PRINGLE, E.G., DIRZO, R. & GORDON, D.M. 2011: Indirect benefits of symbiotic coccids for an ant-defended myrmecophytic tree. – *Ecology* 92: 37-46.
- QUINN, J.L., COLE, E.F., BATES, J., PAYNE, R.W. & CRESSWELL, W. 2012: Personality predicts individual responsiveness to the risks of starvation and predation. – *Proceedings of the Royal Society B-Biological Sciences* 279: 1919-1926.

- RÉALE, D., READER, S.M., SOL, D., MCDUGALL, P.T. & DINGEMANSE, N.J. 2007: Integrating animal temperament within ecology and evolution. – *Biological Reviews* 82: 291-318.
- RÖMER, D. & ROCES, F. 2014: Nest enlargement in leaf-cutting ants: relocated brood and fungus trigger the excavation of new chambers. – *Public Library of Science One* 9: art. e97872.
- RUDGERS, J.A. 2004: Enemies of herbivores can shape plant traits: selection in a facultative ant-plant mutualism. – *Ecology* 85: 192-205.
- SAAR, M., SUBACH, A., REATO, I., LIBER, T., PRUITT, J.N. & SCHARF, I. 2018: Consistent differences in foraging behavior in 2 sympatric harvester ant species may facilitate coexistence. – *Current Zoology* 64: 653-661.
- SCHARF, I., MODLMEIER, A.P., FRIES, S., TIRARD, C. & FOITZIK, S. 2012: Characterizing the collective personality of ant societies: aggressive colonies do not abandon their home. – *Public Library of Science One* 7: art. e33314.
- SEGEV, U., BURKERT, L., FELDMEYER, B. & FOITZIK, S. 2017: Pace-of-life in a social insect: behavioral syndromes in ants shift along a climatic gradient. – *Behavioral Ecology* 28: 1149-1159.
- SIH, A., BELL, A. & JOHNSON, J.C. 2004a: Behavioral syndromes: an ecological and evolutionary overview. – *Trends in Ecology & Evolution* 19: 372-378.
- SIH, A., BELL, A. & JOHNSON, J.C., ZIEMBA, R. 2004b: Behavioral syndromes: an integrative overview. – *The Quarterly Review of Biology* 79: 241-277.
- SIH, A., MATHOT, K.J., MOIRÓN, M., MONTIGLIO, P.-O., WOLF, M. & DINGEMANSE, N.J. 2015: Animal personality and state-behaviour feedbacks: a review and guide for empiricists. – *Trends in Ecology & Evolution* 30: 50-60.
- SUAREZ, A.V., HOLWAY, D.A. & WARD, P.S. 2005: The role of opportunity in the unintentional introduction of nonnative ants. – *Proceedings of the National Academy of Sciences of the United States of America* 102: 17032-17035.
- SUAREZ, A.V., RICHMOND, J.Q. & CASE, T.J. 2000: Prey selection in horned lizards following the invasion of Argentine ants in southern California. – *Ecological Applications* 10: 711-725.
- SUAREZ, A.V., TSUTSUI, N.D., HOLWAY, D.A. & CASE, T.J. 1999: Behavioral and genetic differentiation between native and introduced populations of the Argentine ant. – *Biological Invasions* 1: 43-53.
- THERAULAZ, G. 2014: Embracing the creativity of stigmergy in social insects. – *Architectural Design* 84: 54-59.
- THERAULAZ, G., BONABEAU, E. & DENEUBOURG, J.-L. 1998: The origin of nest complexity in social insects. – *Complexity* 3: 15-25.
- THERAULAZ, G., GAUTRAIS, J., CAMAZINE, S. & DENEUBOURG, J.-L. 2003: The formation of spatial patterns in social insects: from simple behaviours to complex structures. – *Philosophical Transactions of the Royal Society of London. Series A: Mathematical, Physical and Engineering Sciences* 361: 1263-1282.
- THOMAS, M.L., TSUTSUI, N.D. & HOLWAY, D.A. 2005: Intraspecific competition influences the symmetry and intensity of aggression in the Argentine ant. – *Behavioral Ecology* 16: 472-481.
- TSCHINKEL, W.R. 2004: The nest architecture of the Florida harvester ant, *Pogonomyrmex badius*. – *Journal of Insect Science* 4: art. 21.
- TSCHINKEL, W.R. 2005: The nest architecture of the ant, *Camponotus socius*. – *Journal of Insect Science* 5: art. 9.
- TSCHINKEL, W.R. 2015: The architecture of subterranean ant nests: beauty and mystery underfoot. – *Journal of Bioeconomics* 17: 271-291.
- TSUTSUI, N.D. & SUAREZ, A.V. 2003: The colony structure and population biology of invasive ants. – *Conservation Biology* 17: 48-58.
- TURNER, C.H. 1907: The homing of ants: An experimental study of ant behavior. – *Journal of Comparative Neurology and Psychology* 17: 367-434.
- VAROUDIS, T., SWENSON, A.G., KIRKTON, S.D. & WATERS, J.S. 2018: Exploring nest structures of acorn dwelling ants with X-ray microtomography and surface-based three-dimensional visibility graph analysis. – *Philosophical Transactions of the Royal Society B-Biological Sciences* 373: art. 20170237.
- VERZA, S.S., FORTI, L.C., LOPES, J.F.S. & HUGHES, W.O.H. 2007: Nest architecture of the leaf-cutting ant *Acromyrmex rugosus rugosus*. – *Insectes Sociaux* 54: 303-309.
- VONSHAK, M., DAYAN, T. & HEFETZ, A. 2012: Interspecific displacement mechanisms by the invasive little fire ant *Wasmannia auropunctata*. – *Biological Invasions* 14: 851-861.
- WADDINGTON, S.J., SANTORELLI, L.A., RYAN, F.R. & HUGHES, W.O.H. 2010: Genetic polyethism in leaf-cutting ants. – *Behavioral Ecology* 21: 1165-1169.
- WARD, P.S., BRADY, S.G., FISHER, B.L. & SCHULTZ, T.R. 2015: The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). – *Systematic Entomology* 40: 61-81.
- WEBSTER, M.M., WARD, A.J.W. & HART, P.J.B. 2009: Individual boldness affects interspecific interactions in sticklebacks. – *Behavioral Ecology and Sociobiology* 63: 511-520.
- WEIDENMÜLLER, A., MAYR, C., KLEINEIDAM, C.J. & ROCES, F. 2009: Preimaginal and adult experience modulates the thermal response behavior of ants. – *Current Biology* 19: 1897-1902.
- WEIS, J.S. & SOL, D. 2016: *Biological invasions and animal behaviour*. – Cambridge University Press, Cambridge, UK, 367 pp.
- WIERNASZ, D.C., COLE, B.A. & COLE, B.J. 2014: Defending the nest: variation in the alarm aggression response and nest mound damage in the harvester ant *Pogonomyrmex occidentalis*. – *Insectes Sociaux* 61: 273-279.
- WITTE, V., SCHLIESSMANN, D. & HASHIM, R. 2010: Attack or call for help? Rapid individual decisions in a group-hunting ant. – *Behavioral Ecology* 21: 1040-1047.
- WOLF, M. & WEISSING, F.J. 2010: An explanatory framework for adaptive personality differences. – *Philosophical Transactions of the Royal Society B-Biological Sciences* 365: 3959-3968.
- WOLF, M. & WEISSING, F.J. 2012: Animal personalities: consequences for ecology and evolution. – *Trends in Ecology & Evolution* 27: 452-461.
- WRIGHT, T.F., EBERHARD, J.R., HOBSON, E.A., AVERY, M.L. & RUSSELLO, M.A. 2010: Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. – *Ethology Ecology & Evolution* 22: 393-404.