**Title**

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**Author**

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**Publication Date**

2018

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA

Santa Barbara

# How Collective Personality, Behavioral Plasticity, Information, and Fear Shape Collective Hunting in a Spider Society

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Ecology, Evolution and Marine Biology

by

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June 2018

The dissertation of Colin M. Wright is approved.

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April 2018

# ACKNOWLEDGEMENTS

I would like to thank my Ph.D. advisor, Dr. Jonathan Pruitt, for supporting me and my research over the last 5 years. I could not imagine having a better, or more entertaining, mentor. I am very thankful to have had his unwavering support through academic as well as personal challenges. I am also extremely thankful for all the members of the Pruitt Lab (Nick Keiser, James Lichtenstein, and Andreas Modlmeier), as well as my cohorts at both the University of Pittsburgh and UCSB that have been my closest friends during graduate school. I appreciate Dr. Walter Carson at the University of Pittsburgh for being an unofficial second mentor to me during my time there.

Most importantly, I would like to thank my family, Rill (mother), Tom (father), and Will (brother) Wright. Without their support, I would not have been able to return to college to pursue my passion for science. I could not have asked for a more supportive and loving family to return to for the Holidays. I would also like to thank the Hale household (Kayla, Kelly, Shannon, and Ken) for their love and support during my academic pursuits. Some people are not lucky enough to have one loving and supportive family, but I somehow have two.

This dissertation is dedicated to my grandmother, Gerry Hall, though I’ve always known her as *Baba*.

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Colin M. Wright, James L. L. Lichtenstein, Graham A. Montgomery, Lauren P. Luscuskie, and Jonathan N. Pruitt (2017). "Ant presence erases the effect of colony personality and diminishes overall collective foraging in a social spider." *Behavioral Ecology and Sociobiology*

Colin M. Wright, Trevor D. Hyland, Amanda S. Izzo, Donna R. McDermott, Elizabeth A. Tibbetts, and Jonathan N. Pruitt (2017). "*Polistes metricus* queens exhibit personality variation and behavioral syndromes." *Current Zoology*

Colin M. Wright, Vaughan E. Skinker, Amanda S. Izzo, Elizabeth A. Tibbetts, and Jonathan N. Pruitt (2017). "Queen personality type predicts nest guarding behavior, colony size, and the subsequent collective aggressiveness of the colony." *Animal Behaviour*

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Colin M. Wright, Carl N. Keiser, and Jonathan N. Pruitt (2016). “Colony personality composition alters colony-level plasticity and magnitude of defensive behavior in a social spider.” *Animal Behaviour*

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Jonathan N. Pruitt, Colin M. Wright, Carl N. Keiser, Alex E. DeMarco, Matthew M. Grobis, and Noa Pinter-Wollman (2016) "The Achilles' heel hypothesis: misinformed keystone individuals impair collective learning and reduce group success." *Proc. R. Soc. B*.

Carl N. Keiser*, Colin M. Wright*, and Jonathan N. Pruitt (2015). “Warring arthropod societies: social spider colonies can delay annihilation by predatory ants via reduced apparency and increased group size.” *Behavioural Processes*

Colin M. Wright*, Carl N. Keiser, and Jonathan N. Pruitt (2015). “Personality and morphology shape task participation, collective foraging and escape behavior in the social spider *Stegodyphus dumicola*.” *Animal Behaviour*

Andreas P. Modlmeier, Carl N. Keiser, Colin M. Wright, James L. L. Lichtenstein, and Jonathan N. Pruitt (2015). “Integrating animal personality into insect population ecology.” *Current Opinion in Insect Science*

Carl N. Keiser, Colin M. Wright, Nishant Singh, Joseph A. Deshane, Andreas P. Modlmeier and Jonathan N. Pruitt (2014). “Cross-fostering by foreign conspecific queens and slavemaking workers influences individual and colony-level personality.” *Behavioral Ecology and Sociobiology*

Colin M. Wright, C. Tate Holbrook, and Jonathan N. Pruitt (2014). "Animal personality aligns task specialization and task proficiency in a spider society." *Proceedings of the National Academy of Sciences*

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# ABSTRACT

## How Collective Personality, Behavioral Plasticity, Information, and Fear Shape Collective Hunting in a Spider Society

by

Colin M. Wright

The field of animal personality seeks to understand the potential adaptive value of temporally consistent inter-individual differences in behavior. Over the past several decades, this personality framework has helped behavioral ecologists better understand how social groups structure themselves behaviorally, and how intra-colony variation in personality can shape the emergent collective behavior of groups. While studies investigating how collective personalities interact with their environments and influence group survival are becoming more prevalent, research on this topic is still relatively scant. One important aspect of collective personality yet to be given attention is how group personality composition may influence a group's response to invasion by a predator, or how the mere threat of predation can alter the collective behavioral phenotypes of groups. Given the near ubiquity of predation as a selective force in nature, it is important to incorporate both the direct and indirect effects of predators on collective behavior. This will lead to a better understanding about the environmental factors that shape the expression of group personality.

This dissertation approaches these questions using three experiments. The first investigates how the behavioral distribution of colony constituents influences collective behavior in the context of colony defense. This study found that colonies of mixed personality composition exhibited twice as much defensive behavior as other compositions, and that bold compositions were displayed high degrees of behavioral flexibility relative to mixed and shy compositions. The second study observed how prolonged exposure to predators feeds back to determine the collective behavior of groups, and showed that colonies exposed to predators decreased overall collective aggressiveness by half, and eliminated the relationship between personality composition and aggressiveness. The last study investigated how groups prioritize information regarding predator presence when that information is possessed by the majority, or singleton immigrants that vary in leadership traits. This experiment found that groups operate under a "better-safe-than-sorry" strategy, and exhibit cautious collective behavior when any member of their group had been previously exposed to predators. Together, these experiments demonstrate that collective personality is a highly plastic and complex trait, that is determined by a combination if internal (group behavioral composition) and external (environmental risk) factors. Finally, I conclude this dissertation with a comprehensive review on the current state of collective personality research in insects and arachnids.

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# GENERAL INTRODUCTION

The transition from solitary life to living in complex social groups has been described as one of the several major transitions in the evolutionary history of life on earth (Szathmary and Smith, 1995). Despite the intense organizational complexity of such systems, social animals today comprise some of the most successful and numerically abundant species on earth. Though the success of social groups like ants, bees, wasps, and termites is clear, the proximate and ultimate evolutionary mechanisms giving rise to these complex societies has been a central question in both evolutionary biology and behavioral ecology since Darwin's early musings on the topic (Darwin, 1859). Classical theory suggests that individual morphological and behavioral variation plays a key role in structuring differential task participation, task allocation, and division of labor. These properties, taken together, are thought to promote group success via reduced transfer and interference costs, which promote a more streamlined flow of materials within the colony and faster response times to variable work demands (Beshers and Fewell, 2001; Jeanne, 1986; Oster, 1978; Wilson and Sober, 1989). Additionally, these traits are thought to be precipitated via inclusive fitness benefits (Hamilton, 1964), multilevel selection (Nowak et al., 2010; Wilson, 1975), and indirect genetic effects (Wolf et al., 1998). Though the evolution of complex eusocial systems can in principle be explained solely by the benefits garnered from increased colony-level efficiency, the transition to sociality itself can subsequently alter the fitness landscape in which new traits evolve (Moore et al., 1997; Wolf et al., 1999).

One aspect that is intimately related to the success of social groups and can become intensified due to sociality is the ability to effectively combat predation. The methods that social groups deploy to mitigate predation can be either passive or active in nature. For instance, individuals in a group can take advantage of "dilution effects," describing situations where individuals cluster and thereby passively reduce their individual exposure to predators (Dehn, 1990; Foster and Treherne, 1981; Hamilton, 1971; Krause, 1994). Alternatively, a colony or group can mount an active defensive response in a manner that would be simply ineffective if performed by a single individual. Musk oxen (*Ovibos moschatus*), for instance, join together to form a defensive barrier around their young to shield them from wolf predation (Tener, 1954), and eusocial bees and wasps can exhibit swarming behavior in response to predator disturbances (Breed et al., 2004; Judd, 1998). The efficacy of these orchestrated anti-predator responses are often also positively associated with group size (Elgar, 1989; Hermann and Blum, 1981). And, behavioral variation within a colony or group is often thought to help facilitate the execution of many complex tasks, and may for some tasks be even more important than group size *per se* in determining colony success (Keiser and Pruitt, 2014).

The field of animal "personality," defined as consistent differences in behavior between individuals over time and context (Sih et al., 2004), offers researchers a newer and exciting approach for studying animal sociality and its ecology. In the past, much research effort had been expended studying *morphological* variation as being a cause or consequence of division of labor and the benefits it confers. Indeed, a robust literature, both classic and contemporary, surrounds the question of adaptive ratios of castes and subcastes in many social insects (Harvey et al., 2000; Hasegawa, 1997; Herbers, 1980; Oster and Wilson, 1978; Wilson, 1971). Morphological caste differentiation among workers, however, is a relatively rare occurrence taxonomically. Personality variation, in contrast, occurs commonly and has evolved recurrently across a broad swath of animal diversity, including many social taxa (Jandt et al., 2013; Sih et al., 2004; Sih et al., 2012). Only recently have scientists begun investigating how behavioral variation and behavioral plasticity (in lieu of morphological variation) between individuals in monomorphic social species can act as cryptic, yet no less structured or adaptive, *behavioral* castes (Holbrook et al., 2014; Wright et al., 2014a).

My research is broadly concerned with how colony personality composition, keystones presence, and behavioral plasticity interact with predators, and how experience with predators feeds back to potentially mediate both the individual and collective behaviors of an animal society. While each of these several components have been tested in various systems individually (e.g., behavioral composition: (Pruitt, 2013; Pruitt and Riechert, 2011a; Wray et al., 2011); behavioral plasticity: (Holbrook et al., 2014; Oliveira, 2009)), rarely are these attributes tested in concert. A more inclusive treatment exploring how behavioral composition, keystone dynamics, behavioral plasticity and existential threat from predators can combine to either mitigate or facilitate predation *in any social system* is currently lacking.

An excellent model organism for the study of animal personality and sociality is social spiders. These organisms are ideal for addressing many of the above questions because they occur in many regions around the world, vary in their degree of sociality, lack morphological castes, and perform many measurable tasks, such as foraging, nest defense, brood care, and web building that are all important for colony success (Kullmann, 1972; Lubin and Bilde, 2007; Pruitt and Riechert, 2011a; Wright et al., 2014a). The social spider *Anelosimus studiosus*, for instance, exhibits a bimodal distribution of *docile* and *aggressive* behavioral phenotypes (Riechert and Jones, 2008). The behavioral differences in this species have been shown to play a role analogous to morphological castes in some social insects (Wright et al., 2014a). Another social spider, *Stegodyphus dumicola*—the spider that will serve as the model organism for this dissertation—exhibits strong *bold-shy* personality variation within a colony. Boldness is a measure of the propensity of an individual to engage in risky behavior (Sloan Wilson et al., 1994). The distribution of personalities in this species is not bimodal like that seen in *A. studiosus*, but rather a zero-inflated negative binomial distribution with a strong *shy* bias. The rarer *bold* individuals, however, have been shown to act as *keystone individuals* (Modlmeier et al., 2014d): when a single highly *bold* individual is added to a group of all *shy* spiders, it is able to catalyze behavioral variation within the colony, spurring the shyer spiders into action and augmenting their task performance (Pruitt and Keiser, 2014a). Furthermore, this species is commonly preyed upon by a voracious social predator—*Anoplolepis custodiens*, otherwise known as the pugnacious ant (Henschel, 1998; Keiser et al., 2015a). All of these factors, coupled with the fact that this species is easily manipulated in both the field and laboratory, make this system ideal for studying broad questions relating colony personality composition, keystone individuals, and behavioral plasticity to colony success in the lab and field when natural enemies are present.

Chapter I investigates the influence of colony personality composition on collective defense during mock ant raids. Additionally, the stereotyped sequence of handling dangerous prey is observed, as well as the potential protective role their dense retreats may play during ant raids in the field. Chapter II is a study that asks whether predator presence may in turn influence the collective behavior of groups when foraging on both innocuous (moths) and dangerous (ants) prey. Chapter III moves beyond questions pertaining to how personality composition or predator presence influences collective foraging, and instead investigates the role that individual identity (bold vs. shy immigrants), in concert with individual and colony-level information regarding environmental threat, determines collective behavior. And lastly, Chapter IV is a comprehensive review on the current scientific knowledge regarding collective personality in insects and arachnids. This review also includes two tables: one that surveys research on collective behavior performed since 2010, and a second that lists 16 currently untested questions, with corresponding hypotheses, pertaining to collective behavior where big discoveries could be made.

# I. COLONY PERSONALITY COMPOSITION ALTERS COLONY-LEVEL PLASTICITY AND MAGNITUDE OF DEFENSIVE BEHAVIOR IN A SOCIAL SPIDER

## Abstract

The ways in which animal societies respond to threat has enormous consequences for their success. In the present study, we investigated how group personality composition in social spiders (*Stegodyphus dumicola*) alters groups' average response towards predators and how their responses change with experience with important predators, *Anoplolepis custodiens* ants. We found that colonies composed of a mixture of *bold* and *shy* personality types exhibited twice as much defensive web-making behaviour as other colony compositions. Colony defensive behaviour was also more temporally stable following experience with predators for *mixed* colonies than for either monotypic composition (all shy or all bold). Colonies composed of *bold* individuals were particularly erratic in their defensive behaviour over time. Thus, colony composition altered colony-level plasticity in response to experience with one of their most voracious predators. We additionally observed the behaviour of marked individuals within colonies to determine which individual traits were associated with task participation during encounters with predators. Individual morphology was the most reliable predictor of task participation in monotypic colonies, while a combination of personality and morphology predicted task participation in mixed colonies. Lastly, despite a tight association between colony composition and colony defensive behaviour, we found no evidence that colony composition impacted colony survival during ant attacks *in situ*. Instead, older and more established nests were positively associated with colony persistence during attacks.

## Introduction

Animals commonly behave differently in the presence of predators in ways that reduce the chance of their being detected and eaten (David et al., 2014; Lima and Dill, 1990). This is no surprise, as the risk of predation is one of the most ubiquitous selective pressures experienced by any animal. There are many ways in which an organism can avoid predation: camouflage (Merilaita et al., 1999; Stevens and Merilaita, 2009), aposematic coloration (Mappes et al., 2005), non-overlapping activity times (Lima and Dill, 1990; Suselbeek et al., 2014), etc. However, there is perhaps nothing more readily amenable to selection and more immediately advantageous to the organism than modifications to behaviour (Nonacs and Blumstein, 2010). Behaviours, unlike other modes of defense, are rarely constitutive traits and therefore have the ability to be deployed immediately in response to cues of threat via behavioural plasticity (Dingemanse et al., 2010; Holbrook et al., 2014; Sih et al., 2004). Hence, anti-predator behaviour is nearly universal in nature, while morphological adaptations and weapons are, in comparison, less common.

Social organisms provide us with a particularly intriguing landscape for predator-prey interactions. Social organisms can modify their behaviour in response to threat, and have the added complexity of a two-tiered system where behaviour can be simultaneously considered at both the individual and group level. Social organisms often gain protection in numbers, as groups composed of many individuals often exhibit defensive behaviours that would be impotent if performed alone (Breed et al., 2004; Judd, 1998; Tener, 1954). Such effects often positively scale with group size (Elgar, 1989; Hermann and Blum, 1981). Social organisms have also been shown to exhibit varying degrees of behavioural plasticity in response to threat of predation (Holbrook et al., 2014). For instance, some ants (*Lasius pallitarsis*) reduce foraging at sites where they risk predation by larger ant species (Nonacs and Dill, 1990, 1991), and paper wasps often build more nest-defensive structure in areas where predation risk is higher (Furuichi and Kasuya, 2014). Here we will explore how the phenotypic composition of social groups influences their collective defensive behaviour and/or how groups' defensive behaviour changes as a consequence of experience (i.e., repeated exposure to predators). In particular, we consider to what degree a group's personality composition impacts how groups respond to repeated interactions with predators.

A group's personality composition often has a large effect on its collective behaviour (Jandt et al., 2014; Modlmeier et al., 2015a). Here we define animal "personality" as temporally consistent individual differences in behaviour (Sih et al., 2004). The ratios of different personality types with groups are often major determinants of group behaviour in various contexts, as well as group survival and reproductive output (Pruitt, 2013, 2014; Wray et al., 2011). For example, personality variation within a group often helps streamline the performance of collective tasks (Chittka and Muller, 2009; Pruitt and Riechert, 2011a; Waibel et al., 2006; Wright et al., 2014a). In some extreme cases, the effects of personality composition on collective behaviour can outweigh the effects of even large differences in group size (Keiser and Pruitt, 2014). Yet, the majority of the studies published on this topic to date have focused on foraging tasks or interactions with social parasites (Aplin et al., 2014; Burns and Dyer, 2008; Dyer et al., 2009; Gordon, 2013a; Hui and Pinter-wollman, 2014), with infrequent regard for predator-prey interactions, which are arguably some of the most dire interactions groups are likely to endure.

The African social spider, *Stegodyphus dumicola* (Araneae: Eresidae) lives in groups ranging from only one to several thousand individuals. They build webs that consist of a three-dimensional, tough silken retreat permeated with a complex series of tunnels, and two-dimensional capture webs radiating away from this retreat in one or more directions (Seibt and Wickler, 1990). Spiders typically reside within the retreat until they are alerted to prey caught in the capture web via vibrational cues. Unlike the social hymenoptera and termites, *S. dumicola* does not exhibit morphological castes, nor does it seem to display reproductive division of labor. However, this species does exhibit strongly repeatable *bold-shy* personality variation between individuals within the colony. This variation has been shown to predict foraging and escape behaviour at the individual and colony level (Grinsted et al., 2013; Keiser and Pruitt, 2014; Wright et al., 2015). Here we assess how a group's personality composition influences its repeated interactions with their most voracious predators, ants of the genus *Anoplolepis* (*A. custodiens* (Keiser et al., 2015b) and *A. steingroveri* (Henschel, 1998)). Ant raids of spider nests are extremely common where ant and spider ranges overlap, and can often lead to 90-100% colony eradication at sites where ants are active (Henschel, 1998). During ant raids, *S. dumicola* can be observed producing special cribellate silk (Henschel, 1998), which is used to make a tangled silken barrier during attacks.

In the present study we subjected colonies to staged encounters with ant predators to address the following questions: **(1)** Do colonies of different behavioral compositions differ in their anti-predator behaviour? **(2)** Does colony composition influence how colonies alter their behaviour as a single unit (i.e., collective behavioural plasticity) following repeated exposure to predators? Then, by placing colonies within sites with moderate levels of predator density: **(3)** Do differences in colonies' defense behaviour translate to increased persistence during attacks? And lastly, **(4)** is the time spider colonies are allowed to build their retreats positively associated with their ability to withstand ant raids?

## Methods

### *Collection and boldness assays*

Spiders were collected near Upington, Northern Cape, South Africa in January and February of 2015 along roadside bushes and fences. Colonies were placed into cloth bags for transport to our field site near Griekwastad, South Africa. Once at the field site, colonies were sorted and spiders were counted and placed into 500ml plastic containers. Spiders hailing from different source colonies were never mixed, in order to preserve natural levels of within-group relatedness and familiarity (Laskowski et al., in review; Laskowski and Pruitt, 2014a; Modlmeier et al., 2014f). Following colony sorting, we recorded the mass, prosoma width, and boldness of each spider. Boldness is a measure of the propensity of individuals to engage in risky behaviour (Sloan Wilson et al., 1994). Individual boldness here was estimated by administering two rapid puffs of air anteriorly to their prosoma of an isolated spider using a rubber squeeze-bulb. This puff of air simulates attack from a flying predator, and elicits a death-feigning huddle response in *S. dumicola*. Spiders were given a maximum of 600s to resume normal activity and move one body length following the air puff. Bold spiders were defined as those that resume activity between 0-200s, and shy spiders were categorized as those taking 400s or more to resume activity (Keiser and Pruitt, 2014). Boldness has been shown to be highly repeatable in *S. dumicola* ($r > 0.60$) and related species (Keiser et al., 2014a; Keiser et al., 2014c). Each spider was then marked with a unique color combination using fast-drying acrylic modeling paint.

### *Colony construction*

Once morphology (mass and prosoma width) and boldness of all spiders had been recorded, individual spiders (20 spiders per colony) were placed into new 250ml plastic containers with spiders taken from the same source colony. Colonies were constructed with one of three different behavioural compositions: 100% bold (n = 6), 100% shy (n = 27), and 50% bold/50% shy (n = 20). Each colony was given a small *Acacia mellifera* branch to provide substrate for web building. Colonies were then given 24h to construct a capture web and retreat prior to their staged interactions with ants.

### *Colony behaviour during staged predator-prey encounters*

Colony behavioural assays were performed twice a day for three days between 0800 and 1500 hours, totaling six replicates per colony. Each assay was performed as follows: the lid was removed from the colony's container, and the colony was allowed to sit undisturbed for one minute. A single live *A. custodiens* worker was then placed in the center of the colony's capture web. We subsequently recorded the latency and color ID of the first spider to emerge and attack the ant. Additionally, every two minutes for ten minutes (five time points total) we recorded (1) the number and color ID of each spider pinning down the ant's legs, (2) attacking the body, and (3) those participating in defensive cribellate silk making behaviour. Cribellate silk is a very fine silk that is extruded from the cribellum and combed out using a specialized structure called the calamistrum. This silk is wooly in nature, making it efficient at ensnaring insect prey and is therefore commonly used to line capture webs (Vollrath, 2006). In *S. dumicola*, cribellate silk is most commonly produced during the construction and repair of their capture web, but has also been reported to be produced during ant raids. Here the silk is laid down on the attachment points of the colony to the surrounding substrate in areas where predatory ants are abundant (Henschel, 1998). We checked the number of attackers engaged in each of the tasks described above (pinning legs, attacking body, producing cribellate silk) every two minutes for ten minutes (5 checks/trial). The majority of colony members had abandoned the ant carcass by the end of these ten-minute trials.

### *Colony survival experiment: colony composition*

Following completion of our staged predator-prey encounters, each colony was placed haphazardly into the field on *Acacia mellifera* trees after dusk at a site with moderate ant densities. This site was chosen to help ensure that ant raids were common, but not too overwhelming, thus avoiding immediate and total annihilation of all colonies. Colony survival was tracked beginning the following morning when ant activity commenced (roughly 0700 hours). Colonies were checked every hour during daylight to determine when ant raids began for each colony, and the time between the beginning of a raid and colony collapse was recorded. Raids were identified by the presence of many ants gathering outside the colony, biting at silk but not yet infiltrating the spiders' capture web. A colony was considered *collapsed* when ant raids progressed to the point where ants were present inside the spider's retreat, forcing the resident spiders to evacuate.

### *Colony survival experiment: retreat density*

An outstanding question in social *Stegodyphus* pertains to the function of their dense retreat (Seibt and Wickler, 1990). We reasoned that these retreats might play a significant role in mitigating risk during ant raids. To address the question of whether older and, consequently, thicker and denser retreats provide better defense against ant raids, we constructed colonies composed of 100 individuals each that varied in the amount of time that they were allowed to construct retreats. The treatment durations were as follows: one day (*N* = 11), one week (*N* = 10), two weeks (*N* = 12), one month (*N* = 12), and approximately one year (*N* = 18). The one-year colonies were small to medium colonies collected in the field that approximated the size of our artificially constructed colonies (80-120 individuals). All colonies (+ their retreats) were placed within identical plastic containers, and were attached to *A. mellifera* trees during the night. The following morning we recorded the latency between the start of an ant raid and total colony collapse for retreats of different ages. Colony status observations were made every hour during the day when ants are active.

### *Statistical methods*

We used repeated measures ANOVAs to analyze changes in colony defensive paper every two minutes over the course of a single trial (Within-Trial Analysis) and across trials as a consequence of experience (Across-Trial Analysis). Colonies' behaviours at each two-minute check were averaged together for our analysis of colonies' change in behaviour across trials. The predictor variables for these analyses were the three colony behavioural compositions: *shy*, *bold*, and *mixed*. Response variables included the number of spiders pinning legs, the number of spiders attacking the ant's body, and the number of colony members engaged in defensive cribellate silk making. Colony ID and source colony ID were included as random effects in all of our analyses.

For individual task-participation analysis, we used GLMMs with the following predictor variables: individual mass, prosoma width, and boldness as fixed effects and source colony ID and experimental colony ID as random effects. Our individual-level response variables were the number of trials where each individual was the first to emerge and attack, and number of trials where each individual participated in leg pinning, body attacking, or defensive cribellate silk making behaviour.

Survival of colonies in the field was analyzed using a Kaplan-Meier survival function and Mantel-Cox tests in SPSS by IBM. All other statistics were run in JMP 10.

## Results

### *Among-Trial Analysis*

**Latency to emerge and attack**. Over six iterative encounters with predatory ants, all colonies increased their average latency to emerge by nearly 600% (26s on trial 1 vs. 155s by trial 6)(*time*: $F_{5, 53} = 4.9$, $p = 0.0012$). However, colonies' latency to emerge was not associate with their *personality compositions* ($F_{2, 53} = 1.6$, $p = 0.21$) nor did we detect a significant *time*personality composition* interaction ($F_{10, 53} = 0.78$, $p = 0.64$)(Figure 1a). Likewise, latency to attack for all colonies increased over time ($F_{5, 53} = 6.7$, $p < .0001$), with *mixed* and *shy* colonies exhibiting a 400% increase over the six trials, and *bold* colonies showing a nearly 100% increase. On average, *bold* colonies took about twice as long to attack prey as both *shy* and *mixed* colonies every trial (*personality composition*: $F_{2, 53} = 4.2$, $p = 0.02$)(Figure 1b). Here again, we failed to detect a significant *time * personality composition* interaction ($F_{10, 53} = 0.78$, $p = 0.64$).

**Leg pinning**. Over six iterative interactions with predatory ants, all colonies exhibited a 75% decrease in the number of individuals that pinned the ant's legs (*time*: $F_{5, 53} = 5.6$, $p = 0.0005$). This effect was not associated with colonies' *personality composition* ($F_{2, 53} = 1.95$, p

= 0.15) nor did we detect a significant *time * personality composition* interaction ($F_{10, 53}$ = 0.7, p = 0.71) (Figure 1c).

**Body attacking**. Over the six trials, colonies decreased the number of participants that responded by attacking the predator's body by more than 66% (*time*: $F_{5, 53}$ = 2.6, p = 0.039). Additionally, *shy* and *mixed* colonies had nearly twice as many individuals that attacked the body than *bold* colonies (*personality composition*: $F_{2, 53}$ = 3.21, p = 0.049). This result is in stark contrast to the patterns observed when colonies attack prey; when attacking prey, *bold* colonies attack with 200-400% more individuals than *shy* or *mixed* colonies (Keiser and Pruitt, 2014; Wright et al., 2015). The interaction term *time * personality composition* was again not significant ($F_{10, 52}$ = 0.79, p = 0.63)(Figure 1d).

**Defensive cribellate silk making**. Over six trials, colonies exhibited disparate responses to ants in terms of their defensive cribellate silk making behaviour. For example, over the six trials, *shy* and *mixed* colonies displayed relatively stable numbers of cribellate makers, while *bold* colonies presented wildly erratic and unpredictable numbers of individuals engaged in cribellate silk making (*time * personality composition*: $F_{5, 53}$ = 5.8, p = 0.004). Across all compositions, colonies on average decreased the number of cribellate silk makers that they deployed over successive encounters (*time*: $F_{5, 53}$ = 4.38, p = 0.0027). Colonies with different personality compositions differed as well, with *mixed* colonies having twice as many cribellate silk makers than either *shy* or *bold* colonies (*personality composition*: $F_{2, 53}$ = 6.69, p = 0.0028)(Figure 1e).

### *Within-Trial Analysis*

**Descriptive Summary**. Early on, spiders immediately attacked the legs of ant predators, seemingly in order to subdue the predator and to inject venom from a safer distance. Over time, the spiders moved from the legs to attacking the ant's body, where they eventually partially consumed the predator. Defensive cribellate making, in contrast, had few participants early on, but the number of individuals engaged in this activity quickly increased ~6 minutes into the trials (Figure 2).

**Leg Pinning**. For leg pinning behaviour, all colonies exhibited a nearly 75% decrease in the number of individuals pinning the predator's legs over the course of a trial (average # participants = 0.94 vs. 0.25) (*time*: $F_{4, 53} = 11.17$, $p < .0001$). The number of leg pinning individuals did not differ based on a colony's *personality composition* ($F_{2, 53} = 1.41$, $p = 0.25$) nor did we detect a *time* personality composition* interaction ($F_{8, 53} = 1.19$, $p = 0.31$)(Figure 2).

**Body Attacking**. All colonies steadily increased the number of spiders that participated in attacking the ant's body over 10 minute trials (*time*: $F_{4, 53} = 17.8$, $p < .0001$), from an average 0.09 individuals at 2min to 1.46 individuals at 10min. Colonies also differed in participation by composition, with *shy* and *mixed* colonies deploying twice as many individuals that attacked the ant's body than *bold* colonies (*personality composition*: $F_{2, 53} = 3.54$, $p = 0.036$). Here again, this is the opposite trend of what we observe when colonies attack prey; when foraging on safe prey, *bold* colonies attack more rapidly and with many more attackers than *shy* or *mixed* colonies (Keiser and Pruitt, 2014; Wright et al., 2015). Lastly, the interaction term between *time* and *personality composition* was not significant ($F_{8, 53} = 1.25$, $p = 0.27$) (Figure 2).

**Defensive cribellate silk making**. All colonies generally increased the number of cribellate silk making participants by ~200% over 10 minutes (*time*: $F_{4, 53} = 27.4$, $p < .0001$).

Colony compositions also differed in defensive cribellate participation, with *mixed* colonies having twice as many participants of both *bold* and *shy* colonies (*personality composition*: $F_{2, 53} = 9.3$, $p = 0.0003$). The *time * personality composition* interaction term was also highly significant, revealing that *mixed* colonies displayed a much greater acceleration in cribellate participants than either monotypic composition ($F_{8, 53} = 4.16$, $p = 0.0003$).

**Survival**. Colony *personality composition* was not a significant predictor of persistence in a habitat of moderate predatory density ($\chi_{2, 53} = 0.57$, $p = 0.75$)(Figure 3a). In contrast, the age of the colonies' retreat did have a significant impact on their persistence, with individuals taking longer to evacuate older nests ($\chi_{4, 63} = 24.8$, $p < .0001$)(Figure 3b).

### *Individual Task Participation*

**Shy colonies**. For *shy* colonies, none of our predictor variables were associated with individuals' tendency to be the first to emerge or attack an ant predator, nor were any of our predictor variables associated with individuals' tendency to defensively spin cribellate silk. However, individual mass and prosoma width did predict the likelihood for an individual to participate in leg pinning behaviour, with less massive spiders with larger prosomas participating more frequently. Similarly, less massive spiders with larger prosomas also were most likely to participate in attacking the body (Table 1). Thus, large individuals and those in poorer body condition (Jakob et al., 1996) were more likely to attack the predator's legs. Identical patterns of task differentiation were observed when colonies attack prey (Beleyur et al., 2015; Keiser et al., 2014a; Wright et al., 2015).

**Bold colonies**. For *bold* colonies, again none of our predictor variables were associated with whether or not an individual would be the first to emerge, attack, or participate in leg pinning behaviour. For participation in attacking the body, however, a *mass* * *boldness* interaction term was significant, showing that bolder individuals were more likely to participate in this task, but only if they were in poorer body condition. Additionally, less massive spiders with larger prosomas participated more frequently in defensive cribellate silk spinning (Table 1).

**Mixed colonies**. Boldness was the only predictor for individuals' probability of being the first to emerge in response to an ant predator ($F_{1,\ 351} = 5.16$, $p = 0.023$). None of our predictor variables were associated with individuals' tendency to be the first to attack the predator. Additionally, bolder, less massive, and spiders with larger prosomas were more likely to participate in leg pinning, body attacking, and defensive cribellate making behaviour (Table 1). Thus, bolder individuals, larger individuals, and those in poorer body condition were most likely to response to attack predators and to initiate defensive behaviour. Similar patterns of task differentiation are observed in mixed colonies when attacking prey (Wright et al., 2015).

## Discussion

Our study reveals a complex relationship between group personality composition, individual body size indices, and experiential effects in determining how colonies respond to encounters with predators. A multitude of other studies have shown that a group's personality compositions can influence its collective behaviour, although the majority of these studies pertain to foraging tasks (e.g., Aplin et al., 2014; Chang and Sih, 2013; Cote et al., 2011; Dyer et al., 2009; Hui and Pinter-wollman, 2014; Modlmeier et al., 2014a; Modlmeier and Foitzik, 2011). Our data add the more nuanced component that a group's personality composition can also change how groups respond to experience—a sort of *personality composition* by *environment interaction* at the group level. More specifically, colonies of social spiders composed of a mixture of *bold* and *shy* spiders exhibited twice as much defensive cribellate silk making behaviour in response to predators as monotypic compositions. Mixed colonies were also the most consistent in their response across multiple encounters. Bold colonies, in contrast, varied erratically over time in how they responded to predators and were less responsive to predators over all (Figure 1). In contrast, bolder colonies are always more responsive to prey (Keiser and Pruitt, 2014; Pruitt and Keiser, 2014b; Wright et al., 2015). At the level of the individual, we observed that morphological traits and state variables were generally better predictors of task participation in monotypic groups, especially *shy* colonies, and less so in *bold* colonies. For the studies reported here, personality only appears to be a reliable predictor of task participation in behaviourally heterogeneous groups.

Our study is the first to demonstrate that a group's personality composition can alter both its collective behaviour and its behavioural plasticity. While experiential effects on behavioural tendencies are well known at the individual level (Dingemanse et al., 2010; Stamps and Groothuis, 2010a; Stamps and Groothuis, 2010b), relatively little is known about what drives variation in group-level sensitivity or responsiveness to experience (Bengston and Jandt, 2014a; Jandt et al., 2014). Our data demonstrate that group personality composition is one driver in *S. dumicola*. At the individual level, it is often true that more aggressive or bold personality types are less responsive to changes in their environment (Dingemanse et al., 2010; Holbrook et al., 2014; Koolhaas et al., 2007), and there is some evidence of this pattern in social spiders (Holbrook et al., 2014; Modlmeier et al., 2014f). However, our data reveal that colonies composed of bolder (more inflexible) personality types actually exhibit *greater* flexibility in their emergent group-level plasticity, at least, in response to experience with ant predators. This result hints at the possibility that a group of inflexible behavioural types can still produce behaviourally flexible societies. By parallel logic, colonies composed of flexible individuals might exhibit inflexible, stable collective behaviour. This hypothesis receives some circumstantial support from the relatively common finding that behaviourally diverse societies often exhibit greater homeostasis in a variety of collective traits, including behaviour (Burns and Dyer, 2008; Oldroyd and Fewell, 2007). Therefore, we argue that a hypothesized trade-off in behavioural flexibility at the individual vs. group level is deserving of additional scrutiny in this and other test systems.

At the individual level we see a nuanced relationship between colony composition and patterns of task differentiation in response to ant predators (see Table 1). Simply put, individual personality appears to play little to no role in task differentiation in *bold* or *shy* colonies. Rather, we see that morphology and state attributes determine task participation in these monotypic societies, where less massive spiders with larger prosomas participate more frequently in the majority of tasks, including leg pinning (*shy* colonies), attacking the ant body (*shy* and *bold* colonies) or deploying cribellate silk (*bold* colonies). A large prosoma-to-mass ratio is widely considered to reflect poor body condition in spiders (Jakob et al., 1996). Thus, it appears that spiders in poor condition are those that participate more frequently in the majority of tasks, possibly reflecting hunger (argued in Beleyur et al., 2015). Within mixed personality colonies, *bold* individuals and those in poor condition tend to perform the majority of tasks, suggesting some role of personality in organizing task differentiation in heterogeneous groups. This is an intriguing result, because mixed colonies have twice as many cribellate participants as colonies composed of only *bold* individuals, and bold individuals tend to be cribellate silk making specialists. Thus, one would predict an entire colony of *bold* individuals would deploy more cribellate silk makers, not fewer. We therefore propose that something about the presence of unlike, *shy* phenotypes seems to catalyze greater participation by bold individuals. This is counterintuitive to us, because foraging data have repeatedly determined that it is usually bold individuals that enhance the responsiveness of shy individuals, and not *vice versa* (Pruitt and Keiser, 2014b; Pruitt and Pinter-wollman, 2015). This result further echoes a general thread innervating this entire study: the relationships between personality composition, social organization, and collective behaviour in *S. dumicola* appear to switch based on whether colonies are responding to predators or prey. The question of why the patterns appear to reverse when colonies encounter predators is fascinating but yet unknown.

Although we detected no relationship between colony personality composition and survival during ant attacks, we are hesitant to make any impassioned claims about this result, given that no colony survived more than 22 hours. Despite being chosen for its intermediate predation levels, predation pressure at this site is perhaps still too intense to detect any subtle effect of personality composition on colony persistence. Ongoing long-term studies at sites with varying ant densities will provide us with the final critical test. Nest age, however, proved to be somewhat important in determining colony persistence in the field. We reason that this effect is likely quite robust, as we managed to detect them *despite* intense levels of predation.

In conclusion, we have demonstrated that colony personality composition can alter both groups' average response and the way in which colonies respond to experience. We therefore offer that variation in group composition may represent a general factor underlying the way groups behave from moment to moment and their collective behavioural trajectories through time. We again note patterns of task differentiation in *S. dumicola*, this time in regards to the handling of ant predators. As with foraging tasks, a combination of spider's morphological traits and body state are the most consistent contributors to task differentiation, with personality contributing to these patterns in colonies harboring greater within-colony behavioural variation. Lastly, the available data suggest that colony personality composition may not be important for determining colony survival *in situ*, at least at intermediate or high predation sites (Keiser et al., 2015b). Lastly, we see no reasons to suggest our findings should be unique to this system, and encourage other researchers to explore the effects of colony personality composition on collective behaviour and plasticity in their own systems.

## Acknowledgements

Firstly we would like to thank Alex DeMarco for his assistance in the field with this project, and James L. L. Lichtenstein for his advice on previous drafts of this manuscript. This project was supported by the NSF (#1352705 and #1455895 to JNP) and the BSF (BSF 2013086 to JNP).

## Table headers and figure legends:

**Table 1**: Effects tests from a GLMM analysis testing for associations between individuals' traits and their tendency to participate in various aspects of collective foraging against predatory ants in *bold*, *shy*, and *mixed* colony compositions.

**Figure 1**: Graphs depicting the change in response to predatory ants over time by colony composition for (**a**) latency to emerge from the retreat, (**b**) latency to attack, and the propensity to participate in (**c**) leg pinning, (**d**) body attacking, and (**e**) defensive cribellate making behaviour. **Solid** lines correspond to *bold* colonies, **dashed** lines to *mixed* colonies, and **dotted** lines represent *shy* colony compositions.

**Figure 2**: A graph depicting the attack sequence of *S. dumicola* against a threatening insect as a change in the average number of spiders participating in leg pinning (**solid line**), body attacking (**dashed line**), and defensive cribellate making (**dotted line**) over time averaged across all compositions.

**Figure 3**: Kaplan-Meier survival curves depicting the proportion of colonies surviving over time based on (**a**) colony composition, and (**b**) time allowed to construct retreats. For survival curve (**a**), the solid line corresponds to *bold* colonies, the dashed line to *mixed* colonies, and the dotted line represents *shy* colonies. For survival curve (**b**), one-year-old colonies are shown in **orange**, one month colonies in **purple**, two week colonies in **blue**, one week colonies in **green**, and one day colonies in **red**.

**Table 1:**

| | Shy colonies ($N = 529$) | | | | Bold colonies ($N = 115$) | | | | Mixed colonies ($N = 351$) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | n*df* | d*df* | *F* ratio | Prob > *F* | n*df* | d*df* | *F* ratio | Prob > *F* | n*df* | d*df* | *F* ratio | Prob > *F* |
| **First to emerge** | | | | | | | | | | | | |
| Boldness | 1 | 346.5 | 2.98 | 0.085 | 1 | 36.6 | 0.42 | 0.52 | 1 | 345 | 5.16 | **0.023** |
| Mass (g) | 1 | 111.1 | 2.49 | 0.11 | 1 | 45.6 | 0.014 | 0.9 | 1 | 345 | 3.33 | 0.068 |
| Prosoma (mm) | 1 | 429.4 | 2.66 | 0.1 | 1 | 38.9 | 0.008 | 0.92 | 1 | 345 | 2.43 | 0.11 |
| Boldness*Mass (g) | 1 | 483 | 0.019 | 0.88 | 1 | 22.5 | 0.1 | 0.74 | 1 | 345 | 0.076 | 0.78 |
| Boldness*Prosoma | 1 | 464.6 | 0.63 | 0.42 | 1 | 101 | 0.43 | 0.51 | 1 | 345 | 0.42 | 0.51 |
| **First to attack** | | | | | | | | | | | | |
| Boldness | 1 | 250 | 0.49 | 0.48 | 1 | 94.6 | 0.2 | 0.65 | 1 | 345 | 2.53 | 0.11 |
| Mass (g) | 1 | 125.6 | 0.29 | 0.58 | 1 | 98.9 | 1.15 | 0.28 | 1 | 345 | 0.69 | 0.4 |
| Prosoma (mm) | 1 | 417.3 | 3.83 | 0.05 | 1 | 108 | 0.044 | 0.83 | 1 | 345 | 0.24 | 0.61 |
| Boldness*Mass (g) | 1 | 429.4 | 0.004 | 0.94 | 1 | 85.8 | 1.35 | 0.24 | 1 | 345 | 0.31 | 0.57 |
| Boldness*Prosoma | 1 | 392.4 | 0.3 | 0.57 | 1 | 107. | 0.38 | 0.53 | 1 | 345 | 0.43 | 0.5 |
| **Leg pinning** | | | | | | | | | | | | |
| Boldness | 1 | 405.6 | 0.031 | 0.86 | 1 | 104. | 0.1 | 0.74 | 1 | 336 | 4.55 | **0.033** |
| Mass (g) | 1 | 407.5 | 10.98 | **0.001** | 1 | 107. | 1.15 | 0.28 | 1 | 243. | 5.71 | **0.017** |
| Prosoma (mm) | 1 | 514.1 | 11.46 | **0.0008** | 1 | 107. | 0.0049 | 0.94 | 1 | 341. | 7.88 | **0.0053** |
| Boldness*Mass (g) | 1 | 499 | 0.26 | 0.6 | 1 | 102. | 0.096 | 0.75 | 1 | 339. | 1.12 | 0.28 |
| Boldness*Prosoma | 1 | 486.3 | 0.19 | 0.65 | 1 | 105. | 0 | 0.99 | 1 | 335. | 1.14 | 0.28 |
| **Body attacking** | | | | | | | | | | | | |
| Boldness | 1 | 520.1 | 0.69 | 0.4 | 1 | 101. | 1.5 | 0.22 | 1 | 332. | 6.17 | **0.013** |
| Mass (g) | 1 | 476.1 | 8.1 | **0.0047** | 1 | 105. | 0.33 | 0.56 | 1 | 313. | 11.1 | **0.0009** |
| Prosoma (mm) | 1 | 517 | 8.18 | **0.0044** | 1 | 108. | 0.18 | 0.67 | 1 | 337. | 8.41 | **0.004** |
| Boldness*Mass (g) | 1 | 510.6 | 0.000 | 0.98 | 1 | 99.1 | 5.76 | **0.018** | 1 | 334. | 0.14 | 0.7 |
| Boldness*Prosoma | 1 | 511.2 | 0.003 | 0.95 | 1 | 106. | 0 | 0.99 | 1 | 331. | 0.021 | 0.88 |
| **Cribellate making** | | | | | | | | | | | | |
| Boldness | 1 | 514.8 | 0.23 | 0.63 | 1 | 108 | 0.13 | 0.71 | 1 | 331. | 14.3 | **0.0002** |
| Mass (g) | 1 | 487.6 | 1.88 | 0.17 | 1 | 108 | 4.03 | **0.047** | 1 | 316 | 8.31 | **0.0042** |
| Prosoma (mm) | 1 | 511 | 0.96 | 0.32 | 1 | 105 | 11.4 | **0.001** | 1 | 334. | 9.06 | **0.0028** |
| Boldness*Mass (g) | 1 | 505.2 | 0.16 | 0.68 | 1 | 108. | 0.28 | 0.59 | 1 | 332. | 0.19 | 0.66 |
| Boldness*Prosoma | 1 | 505.6 | 1.17 | 0.27 | 1 | 104. | 0.011 | 0.91 | 1 | 330. | 0.98 | 0.32 |

**Figure 1**:

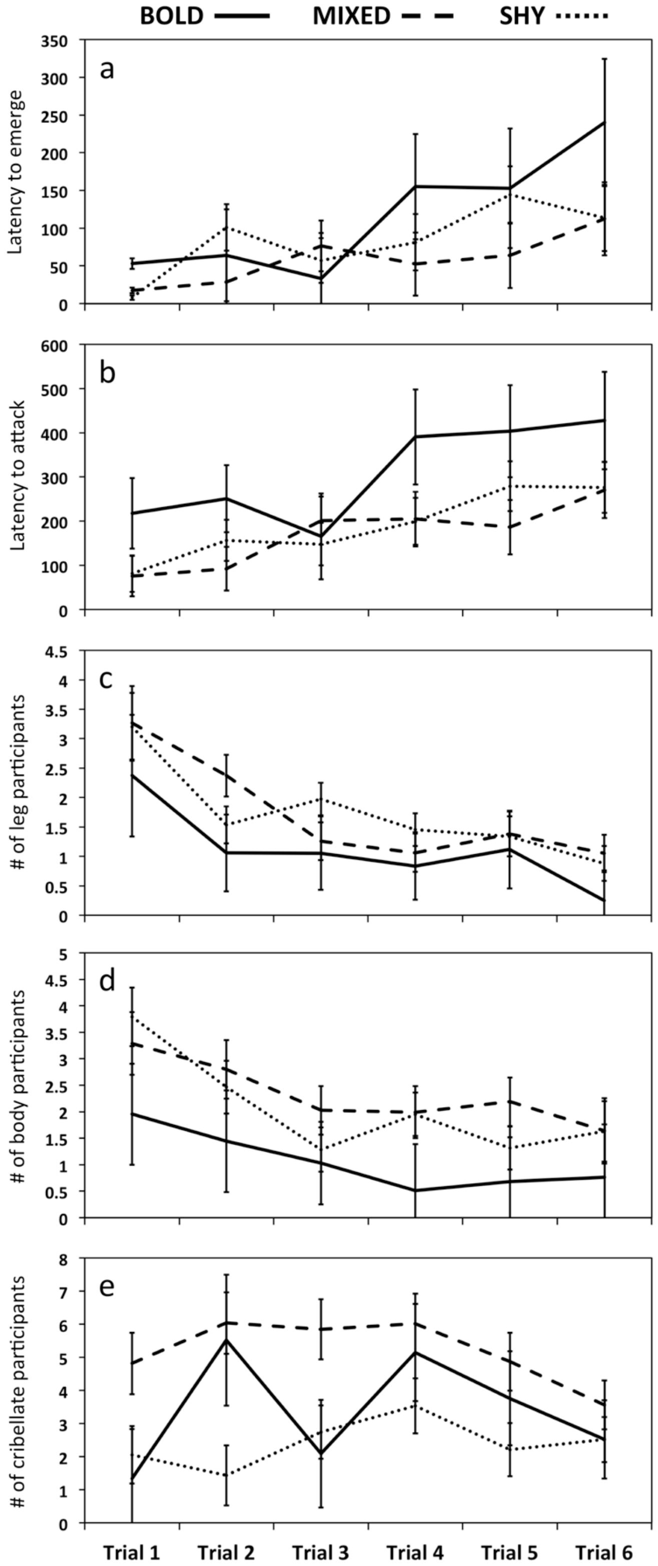

BOLD
MIXED
SHY
a
Latency to emerge
0
50
100
150
200
250
300
350
b
Latency to attack
0
100
200
300
400
500
600
c
# of leg participants
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
d
# of body participants
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
e
# of cribellate participants
0
1
2
3
4
5
6
7
8
Trial 1
Trial 2
Trial 3
Trial 4
Trial 5
Trial 6

**Figure 2**:

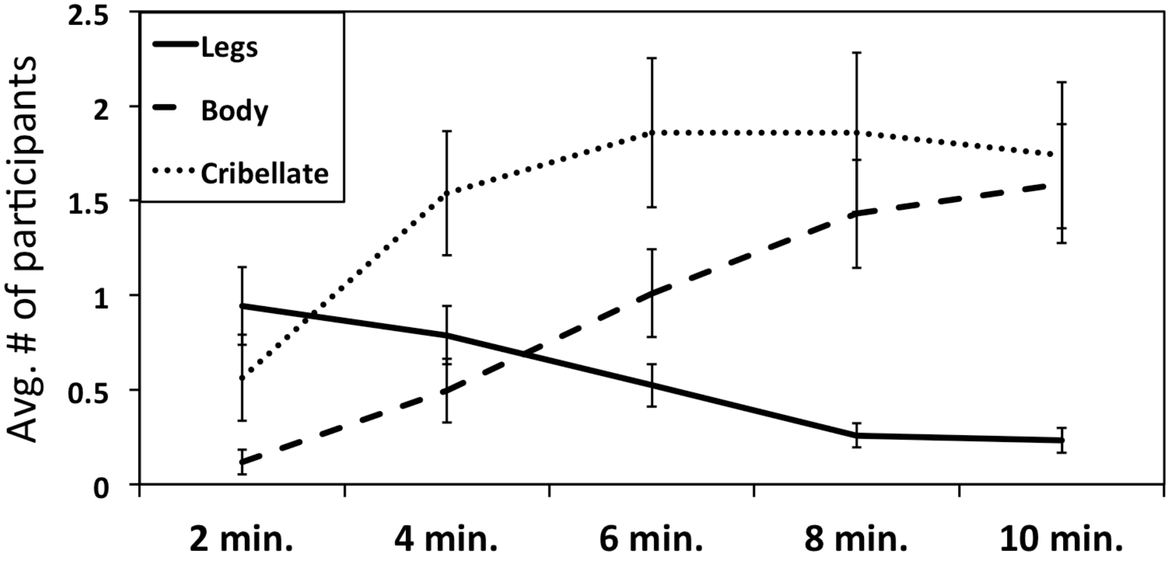
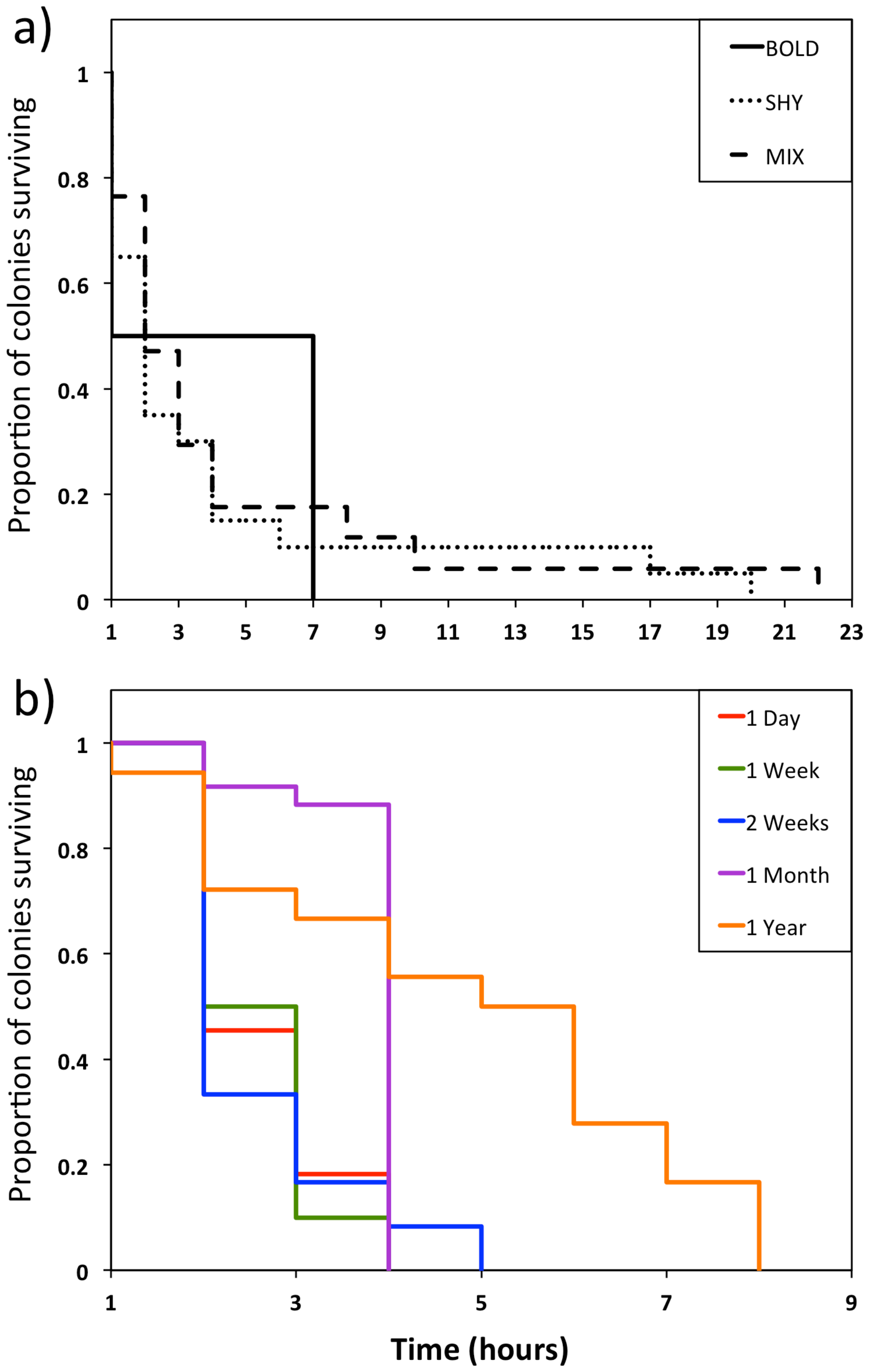

Avg. # of participants
2.5
2
1.5
1
0.5
0
Legs
Body
Cribellate
2 min.
4 min.
6 min.
8 min.
10 min.

**Figure 3**:


a)
Proportion of colonies surviving
1
0.8
0.6
0.4
0.2
0
1
3
5
7
9
11
13
15
17
19
21
23
BOLD
SHY
MIX
b)
Proportion of colonies surviving
1
0.8
0.6
0.4
0.2
0
1
3
5
7
9
Time (hours)
1 Day
1 Week
2 Weeks
1 Month
1 Year

# II. EXPOSURE TO PREDATORS REDUCES COLLECTIVE FORAGING AGGRESSIVENESS AND ELIMINATES ITS RELATIONSHIP WITH COLONY PERSONALITY COMPOSITION

## Abstract

Predation is a ubiquitous threat that often plays a central role in determining community dynamics. Predators can impact prey species by directly consuming them, or indirectly causing prey to modify their behavior. Direct consumption has classically been the focus of research on predator-prey interactions, but substantial evidence now demonstrates that the indirect effects of predators on prey populations are at least as strong as, if not stronger than, direct consumption. Social animals, particularly those that live in confined colonies, rely on coordinated actions that may be vulnerable to the presence of a predator, thus impacting the society's productivity and survival. To examine the effect of predators on the behavior of social animal societies, we observed the collective foraging of social spider colonies (*Stegodyphus dumicola*) when they interact with dangerous predatory ants either directly, indirectly, or both. We found that when colonies were exposed directly and indirectly to ant cues, they attacked prey with approximately 40-50% fewer spiders, and 40-90% slower than colonies that were not exposed to any predator cues. Furthermore, exposure to predatory ants disassociated the well-documented positive relationship between colony behavioral composition (proportion of bold spiders) and foraging aggressiveness (number of attackers) in *S. dumicola*, which is vital for colony growth. Thus, the indirect effects of predator presence may limit colony success. These results suggest that enemy presence could compromise the organizational attributes of animal societies.

## Introduction

Predator-prey interactions are one of the most widely studied phenomena in ecology because of their importance in driving community dynamics (Berryman, 1992; Murdoch et al., 2003; Williams et al., 2004). Traditionally, studies of predator-prey interactions have focused on how predators capture and consume prey and the effects of this consumption on prey populations. The effects of direct consumption on prey populations are referred to as *consumptive* effects or *density mediated interactions*. An alternative approach to examining predator-prey interactions was to address the *non-consumptive* effects of predators. These indirect effects include changes to the behaviors of prey species, such as dispersal, foraging times, general activity level, etc. (Bell and Sih, 2007; Cote et al., 2013; Lima, 1998; Lima and Dill, 1990), or induced morphological, developmental, or physiological costs (Barry, 1994; Downes, 2001; Orrock et al., 2008; Werner and Peacor, 2003) in response to perceived predation risk or intimidation. These *non-consumptive* effects can influence prey populations directly and through changes to trophic interactions. Non-consumptive predator effects are sometimes called *trait-mediated interactions*. Evidence from several meta-analyses that each estimated the magnitude of consumptive and non-consumptive effects, and total effects of predators on prey survival and density, have demonstrated that the non-consumptive effects on predator-prey interactions can be at least as strong as, or even substantially stronger than, consumptive effects (Orrock et al., 2008; Preisser et al., 2005; Werner and Peacor, 2003). Both density mediated and trait mediated interactions, taken together, now form an integrative approach regarding how predators and prey interact, and the effects these interactions have on population dynamics.

The field of animal personalities, which investigates the ecological effects of consistent individual differences in behavior within a population or group, has proven effective at explaining many inter- and intra-specific interactions (Modlmeier et al., 2015a; Sih et al., 2004; Sih et al., 2012), including predator-prey dynamics (Bell and Sih, 2007; Cote et al., 2013; Sih et al., 1990). Common personality axes include aggressiveness/docility, boldness/shyness (or the degree to which individuals engage in risky behavior), sociability, activity level, or the degree to which individuals explore novel environments. Most studies on predator-prey interactions are performed on species of solitary or gregarious animals (Bell and Sih, 2007; Castellanos and Barbosa, 2006; Clinchy et al., 2013; Cote et al., 2013; David et al., 2014). However, personality studies investigating social taxa have revealed the presence of stable differences in behavior at both the individual and group level (Bengston and Jandt, 2014b; Jandt, 2013; Wright et al., 2016b). The extent to which behavioral variation at either or both of these levels influences predator-prey interactions, or any other kind of species interaction for that matter, has been little explored.

Predator-prey interactions where the predator, prey, or both are cooperative organisms offer an intriguing case study for examining how the collective personalities of either predator or prey might impact species interactions and outcomes. For instance, when a colony of social organisms is the target of predation, the outcome can range from colony annihilation to successful predator evasion, without or with individual casualties. Notably, the losses that a group sustains during an attack by a predator may reduce its capacity to combat future predation attempts or to reproduce, akin to leg or tail autonomy in response to predation in individual organisms. Such losses may further curtail a group's ability to effectively perform the various tasks necessary for colony function and growth, such as resource acquisition and care for offspring (Oster, 1978). Losses sustained by cooperative hunting groups while attacking prey may reduce their ability to successfully overwhelm future prey. Recent data on colony-level personality in fish (Jolles et al., 2015), social arachnids (Keiser and Pruitt, 2014), and eusocial insects (Modlmeier and Foitzik, 2011; Wright et al., 2016a) suggest that the way prey colonies respond to such attacks might be vary across groups, and conversely, that mere presence of predators may alter colonies' behavioral tendencies in ways that impacts their performance in other contexts (e.g., foraging efficiency, hygienic behavior). Colony

While the effect of predators on group size (direct consumption) has been examined (Krause and Godin, 1995), there has been little work on whether the presence of a predator may indirectly disrupt the organization and coordination of group activities. Given that groups can possess traits that individuals cannot (such as adaptive personality ratios and emergent behaviors), observing how predator presence impacts these collective traits could prove illuminating. For instance, many groups rely on complex organization and cooperation to successfully meet an array of ecological challenges to perform tasks such as collective foraging (Beshers, 2001; Bonabeau et al., 1998; Camazine et al., 2001; Deneubourg et al., 1990; Robinson, 1992). Examining how predators affect the collective traits of their prey could therefore enhance our understanding of the ecology of social animals in particular, as well as why the broader ecological impacts of social animals may vary through space and time.

### *Study system and questions*

The African desert social spider, *Stegodyphus dumicola*, is abundant and occurs throughout southern Africa. These spiders build dense three-dimensional silken retreats that are permeated with numerous tunnels where the spiders lay their eggs and reside for protection (Seibt and Wickler, 1990). Multiple two-dimensional capture webs radiate away from this central retreat, and spiders are recruited to the capture webs through vibrational cues produced by ensnared and struggling prey (Amir et al., 2000; Whitehouse and Lubin, 1999). These spiders are a tractable system for evaluating the magnitude of non-consumptive effects on group behavior because spider groups rely on the ability of their constituents to organize hunting groups to subdue large and occasionally dangerous prey (Keiser and Pruitt, 2014; Wright et al., 2015). This species also exhibits a high degree of intracolony behavioral (or personality) variation that is predictive of colony performance in foraging (Grinsted et al., 2013), defensive behavior (Wright et al., 2016a), web repair (Keiser et al., 2016c), bacterial transmission rates (Keiser et al., 2016a; Keiser et al., 2016b), and task differentiation among colony constituents (Wright et al., 2015). In fact, colony behavioral composition is more important than colony size for predicting foraging aggressiveness and efficiency in this species (Keiser and Pruitt, 2014). Additionally, *S. dumicola* colonies are frequently raided by pugnacious ants (*Anoplolepis custodiens*), a voracious social predator that is the main cause of death for established *S. dumicola* colonies in nature, wherever these species' ranges overlap (Henschel, 1998; Keiser et al., 2015b; Wright et al., 2016a).

The defensive behavior of *S. dumicola* towards *Anoplolepis* ants hints at an important evolutionary history between these species. *S. dumicola* colonies exhibit a unique, stereotyped defensive behavior when ants lay siege to the colony: the spiders immediately begin producing cribellate silk that they then use to ensnare individual ants and to construct tangled silken barriers that help prevent the advancement of ant workers into the spiders' vulnerable retreat (Henschel, 1998; Wright et al., 2016a). Cribellate barriers are constructed prophylactically at the attachment points of colonies to the surrounding substrate in regions where ant raids are particularly common (Henschel, 1998). Previous studies have shown that the magnitude of this defensive response depends on the colony's personality composition, where colonies composed of a mixture of bold and shy spiders exhibited twice as much defensive cribellate making as monotypic colonies (Wright et al., 2016a). *S. dumicola* colonies attack *A. custodiens* workers progressively slower and with fewer individuals after repeated exposures to dangerous ants in the lab, and colonies receiving ant treatments exhibit a reduction in mass gain (Pruitt et al., 2016; Wright et al., 2016a). This stands in contrast to how colonies behave when they forage on an innocuous prey item, such as a moth. Under these conditions, colonies attack progressively faster after repeated exposures and do not lose significant mass (Pruitt et al., 2016). Thus, it is clear that *S. dumicola* colonies can acquire information about their environment during foraging bouts, and are able to adjust their foraging behavior depending on the representation of innocuous vs. dangerous prey in their environment. Yet, it is unknown whether *S. dumicola* colonies can acquire information about predator presence/absence using indirect methods (e.g., via chemical cues), without physically interacting with the predator. Such an ability could have substantive benefits if early detection proves important in preparation for a raid or (Kleeberg et al., 2014), conversely, this ability could have appreciable costs if predator presence causes individuals or groups to behave suboptimally.

The fact that *S. dumicola* relies so heavily on complex and well-orchestrated collective behaviors to execute important tasks make this species ideal to evaluate the effects predator presence may have on colony organization and performance. Here we hypothesize that the threat of predation may negatively impact any number of these organizational traits, such as decreasing colony responsiveness towards prey vibratory cues or the number of attackers that respond to prey (Harwood and Aviles, 2013), thus adversely impacting colony performance.

To uncover how predators influence the collective behavior of their prey, we constructed experimental colonies that varied continuously in their proportion of bold versus shy individuals that composed them.  We tested the collective prey capture of groups of different behavioral composition before subjecting them to either direct, indirect, direct + indirect, or no predatory cues and reevaluated their collective behavior every five days to assess whether and how interactions with ants altered spiders' foraging aggressiveness. In addition to tracking colony behavior over time, we also collected data on membership mortality, and the average change in mass in colony constituents.

## Methods

### *Collection and measurement*

Spider colonies were collected from Upington, South Africa in October 2015. Colonies were brought into the lab, and each spider was individually isolated from its nestmates in 30ml plastic condiment containers. Once isolated, we measured the boldness of each spider by administering two puffs of air to their anterior prosoma using a rubber squeeze-bulb. Boldness is defined as the propensity of an individual to engage in risky behavior (Sloan Wilson et al., 1994). The puffs of air simulate an attack from an avian predator, and cause the spider to pull its legs toward its body and huddle (Pruitt et al., 2013; Riechert and Hedrick, 1990). The latency to unhuddle and move one whole body length following this aversive stimulus is our measure of boldness. We operationally define *bold*, *intermediate*, and *shy* individuals as those having latencies between 0-199, 200-399, and 400-600 seconds, respectively (Keiser et al., 2014b). These boldness scores are then subtracted from 600 (the maximum value) so that higher numbers reflect greater boldness scores.

Following boldness assays, we measured the mass and prosoma width of each spider. The body condition of each spider was estimated as its residual from a linear regression of mass versus body size, measured as prosoma width, for all spiders in our study (Jakob et al., 1996). Using this technique, positive values indicate spiders that are heavier for any given prosoma width, and negative values indicate spiders that are relatively lighter for their prosoma width. At the end of the experiment, we re-measured the mass and prosoma width of each spider, to examine whether predator-exposure treatment had an effect on average body condition.

### *Colony composition*

Following boldness, mass, and prosoma measurements, we constructed a total of 84 colonies (21 colonies per treatment group) containing 20 spiders each. Each experimental colony was derived from a single source colony, and spiders from different source colonies were never mixed, to preserve natural levels of within-group relatedness and familiarity (Laskowski et al., 2016a; Laskowski and Pruitt, 2014b; Modlmeier et al., 2014e). Each of the 21 colonies per treatment group varied along a gradient in the proportion of *bold* and *shy* individuals contained within the colony (from 100% *bold* to 100% *shy* and every composition in-between). For example, the first colony contained only 20 bold spiders, the next colony contained 1:19 shy:bold, followed by 2:18 shy:bold, and so on, ending with a colony containing only 20 shy spiders. Each colony was housed in a 230ml plastic cup with a lid and contained three *Acacia mellifera* twigs as web-building substrate. We assigned each colony to one of the following four treatment groups: (1) exposed to ants indirectly, (2) daily direct exposure to ants in the capture webs, (3) both direct and indirect exposure to ants, and (4) neither direct nor indirect cues (control) (in a 2 x 2 design). Colonies were provided 24 hours to construct capture webs prior to any ant exposures providing sufficient time to construct a retreat structure and a small capture web within the enclosure.

To expose colonies indirectly to ants, five *A. custodiens* workers were placed in a 230ml cup with water and sugar. The cup of the experimental spider colony was then stacked on top of the ant cup, containing the ants, sugar, and water in the small space (10mm high) between the two stackable cups. We punched many small holes in the bottom of the spider colony cup to allow indirect cues, such as chemical compounds, to permeate into the spider nest. For treatments that were allowed to interact only directly with ants, a single *A. custodiens* worker was placed in the center of the capture web once daily. Spiders were allowed to attack and subdue the ant, but the ant was removed from the colony before the spiders were able to consume them. These colonies were stacked on top of cups containing water and sugar, but no ants. Colonies exposed simultaneously to both direct and indirect ant cues were stacked on cups containing ants, sugar and water, and received an ant in their capture web once daily. Lastly, our control colonies were stacked inside cups that contained only sugar and water, and never received direct or indirect ant cues.

### *Colony aggressiveness*

To assess each colony's baseline aggressiveness in response to prey prior to manipulation, all colonies were assayed for colony level aggressiveness in prey capture four times over two days prior to setting up our treatment groups. To assess colony aggressiveness, we placed a small piece of white paper (1x1cm) in the center of the colony's capture web. Colonies were given a 30 second acclimation period following this initial disturbance. We then vibrated the paper using a handheld vibrator, which causes the paper to flutter about, resembling a struggling winged insect. We recorded the latency for the first spider to attack the paper, as well as the number of attacking spiders on the capture web at the moment the paper was first attacked. These values give us a measure of both the speed and magnitude of prey attack each colony exhibits. After assigning colonies to the various predator-exposure treatments, we re-measured colony level aggressiveness four more times every five days, to determine the impacts of our predator-exposure treatments on colony aggressiveness over time (i.e. whether differences were exacerbated or perhaps attenuated through habituation). Colonies were given a maximum of 5 minutes to attack the simulated prey item. All colonies were fed a single, dead, previously frozen and thawed termite worker (to ensure termites did not damage capture webs), every three days over the course of the experiment. We removed termite corpses the following day to reduce clutter in the capture webs, which could subtly influence colony behavior due to their propensity to vibrate during mock prey trials using the vibratory device.

Blinded methods across treatments were not used, given that it was necessary to spatially separate treatment groups so as not to inadvertently contaminate other treatments with indirect (chemical) ant cues. Therefore, we knew which treatment groups we were testing during observations. However, within each treatment group, the experimenter was blind to colony ID during observations, and thus data obtained on relating to group composition was gathered blind. Please see Supplementary Table (S1) for the complete experimental timeline.

### *Statistical analysis*

To assess whether our treatment groups impacted colonies' aggressiveness measured as their latency to attack or the number of attackers deployed in response to a novel prey stimulus over time, we used normally distributed GLMMs with an identity-link function.

Inspection of Q-Q plots and the distribution of the model residuals conveyed a strong fit for this model structure. We included time (day number), treatment, and a treatment × time interaction term as predictor variables in our model. “Time” is a categorical variable denoting the day number the behavioral assessments occurred, such as colony aggressiveness on day 0, day 5, day 10, and day 15. Source colony ID and experimental colony ID nested within source colony ID were included as random effects. A significant interaction term between trial number and treatment indicates that colonies change in their response over time as a result of their treatment group. Post hoc comparisons for latency to attack and number of attackers were performed between each treatment group at each time point using Tukey’s HSD groupings. We performed an additional analysis at each time point using 2-Way ANOVAs to determine whether any interaction between exists between direct and indirect effects, and their relative importance.

Previous studies have shown a strong correlation between the proportion of bold spiders within a colony and both the latency to attack and average number of attackers. We used multiple bivariate linear regressions to verify this relationship in each treatment group prior to any ant exposures, and again at each time point to observe how this relationship may change with exposure to predators. We compared our initial observations (day 0) to our final observations (day 15) using ANCOVAs in order to determine whether the relationship between colony composition and foraging aggressiveness changed before vs. after extended exposure to predatory ants.

To determine the potential effects of predator-exposure treatments on spider mortality (measured as the number of dead individual spiders found in each colony at the end of the experiment), and change in body condition, we again used GLMMs with a normal distribution and identity-link function with source colony ID and experimental colony ID nested within source colony ID included as random effects. All statistics were performed in JMP 12, by SAS. An independent model was created for both of these colony performance metrics (mortality and change in body condition).

## Results

### *Effects of treatment on number of attackers and latency to attack*

Exposure to any predator cues decreased the magnitude of prey attacks over time, which could impair the colony's ability to capture large prey. All colonies that received direct, indirect, or both predator cues displayed a decrease of up to 50% in the number of attackers that responded to simulated prey relative to the control colonies (whole model: $p < 0.0001$)(Figure 1). Indirect cues were also over 2.5X more effective than direct cues in influencing colony behavior when comparing LogWorth, which is defined as –log(p-value), and is used to show the relative strengths of predictor variables (direct vs. indirect effects in this case). All colonies, including the control treatment, showed an increase in latency to attack the simulated prey over time (day #: $p = 0.0001$). However, treatments that received any ant cue attacked slower on average than control colonies (treatment: $p = 0.0077$). The interaction term Time * Treatment was not significant ($p = 0.29$) indicating that treatments only differed in their average attack latencies, and these differences did not change over time (Figure 2). Post hoc comparisons between treatment groups at each time point did not reveal significant differences in latency to attack at any one time point. See Table 1 for the full model outputs, Table 2 for comparisons between treatment groups at each time point, and Table 3 for 2x2 analyses. In short, exposure to any predatory cue reduced the magnitude and speed at which colonies attack prey, and indirect cues proved to be over 2.5 times more important than direct cues in influencing colony behavior.

*Effects of personality composition and treatment on prey attack*

The well-documented, positive association between the proportion of bold spiders in a colony and collective foraging disappeared over time for colonies that were exposed to predator cues. On day 0, prior to exposing any colonies to predator cues, all colonies displayed the characteristic positive relationship between the proportion of bold spiders within the colony and the number of attackers that were deployed in response to prey (Keiser et al 2014). However, this positive relationship gradually diminished in all experimental colonies over time following exposure to ants (indirectly, directly, or both), while the relationship was maintained in control colonies (Figure 3). Comparisons between the slopes at day 0 versus day 15 for each treatment group independently using ANCOVA further suggests that the effect of colony personality composition on the number of individuals that respond to prey decays over time in some treatments groups (control: $F_{1,42} = 0.23$, $p = 0.63$; indirect cues: $F_{1,42} = 12.2$, $p = 0.0012$; direct cues: $F_{1,42} = 0.75$, $p = 0.39$; both direct and indirect cues: $F_{1,42} = 6.02$, $p = 0.018$). Most notably, this change over time was only significant for treatments where ants were placed beneath the colony (i.e. those colonies provided with indirect cues) but not for control colonies or colonies that only interacted with ants directly on the capture web. This result conveys that the persistent exposure to indirect cues of nearby ants is key in ablating the collective aggressiveness of *S. dumicola* societies composed of bold spiders. For latency to attack, no clear patterns emerged over time or between treatments.

*Mortality and body condition*

We did not observe any significant differences between ant exposure treatment groups in mortality rate ($\chi^2_3 = 1.86$, $p = 0.60$), or change in body condition ($\chi^2_3 = 0.76$, $p = 0.85$).

## Discussion

Our study demonstrates that the non-consumptive effects of predatory ants may impair the foraging efficiency of *S. dumicola* colonies, which may in turn reduce colony success. When spider colonies were exposed directly or indirectly to ant cues, *S. dumicola* colonies attacked prey with 40-50% fewer spiders, and at speeds that were 40% to 90% slower than control colonies. This finding is important because *S. dumicola* colonies, like other social spiders, require quick attack speeds to reach prey before they can escape, and colonies rely on deploying large numbers of spiders to successfully overwhelm large or dangerous prey items (Harwood and Aviles, 2013; Pruitt and Riechert, 2011a). More broadly, spider societies are thought to have evolved because of their ability to subdue large and particularly profitable prey that are unavailable to singleton spiders (Agnarsson et al., 2006; Aviles and Purcell, 2012; Nentwig, 1985; Powers and Aviles, 2007; Yip et al., 2008). In fact, large colonies require very large prey to persist (Yip et al., 2008). We consequently reason that exhibiting a 40-90% reduction in attack speed and a 50% reduction in the number of attackers could diminish a colony's ability to capture prey and, consequently, reduce colony growth and overall fitness. Furthermore, indirect exposure to ant cues alone was sufficient to drastically reduce colonies' responsiveness towards prey, and proved to be more than 2.5 times more important than indirect cues in influencing colony behavior. So, colonies that never directly experience an ant raid may still suffer by simply residing in proximity to these predators.

Our results further revealed that ant presence, in addition to their negative effects on colony foraging speed and intensity (Figures 1 and 2), weakens the relationship between colony personality composition and foraging aggressiveness (number of attackers) in *S. dumicola* (Figure 3). Past studies have demonstrated a strong positive relationship between the proportion of bold spiders within a colony and the number of attackers that respond during foraging events. Our results demonstrate that this effect vanishes when *S. dumicola* colonies are exposed to cues of predatory ants. In particular, it seems that persistent, indirect cues are necessary and sufficient for weakening this well-established relationship: indirect cues proved more consequential than direct cues in diminishing the link between colony composition and foraging aggressiveness (Figure 3). The sufficiency of indirect cues to alter colony behavior hints at a long evolutionary history with these dangerous predators.

These findings suggest that the presence of predatory ants could weaken the role of bold spiders in *S. dumicola* colonies as "keystone individuals" (Modlmeier et al., 2014d). Adding a single, highly bold spider into a colony composed of only shy spiders dramatically decreases colonies' latency to attack and increases the number of attackers that respond to prey (Pruitt et al., 2013; Pruitt and Keiser, 2014a). Bold spiders appear to achieve this social influence by catalyzing aggressiveness in their otherwise shy, non-aggressive group mates, eventually leading to a lasting shift in colonies' behavioral composition (Pruitt et al., 2013; Pruitt and Keiser, 2014a; Pruitt and Pinter-Wollman, 2015). The degree to which keystones catalyze this behavioral variation is directly proportional to the magnitude of their boldness scores (Pruitt and Keiser, 2014a) and the length of time these individuals remain in the group (Pruitt and Pinter-Wollman, 2015). Having just one bold individual also increases colonies' collective mass gain and survival in laboratory conditions (Lichtenstein et al., 2016b; Pruitt and Keiser, 2014a). Thus, *S. dumicola* colonies may only gain the benefits of bold keystone individuals in environments where *Anoplolepis* ants (or perhaps a wide range of other predators or risky cues) do not occur, or are rare. Populations of *S. dumicola* and *A. custodiens* are both ephemeral and patchy, so many regions exist where one, both, or neither species occur. Field studies that span across a diversity of environments are needed to critically evaluate these hypotheses.

Ant presence did not appear to affect any measure of colony growth that we considered, including individual mortality rates, or average changes in body condition. However, given the short duration of our study (two weeks), we are hesitant to state definitively that ant presence does not influence any of these elements. It might merely take more time, or the ill effects might only appear under a limited set of conditions. For instance, high stress environments have been known to shorten life spans and generate weight loss in many species (Clinchy et al., 2013; Perez-Tris et al., 2004; Thomson et al., 2010). It is possible that our feeding regime, a termite every three days, was overly generous and consequently negated any predator-induced stress effects on colony performance. More restricted diets, longer-term experiments, or both, might reveal nuanced performance effects. Alternatively, ant presence might not cause spiders sufficient physiological stress to reduce their performance.

In summary, we provide experimental evidence that the mere presence of predators can alter and possibly impair the collective foraging traits of complex animal societies. Specifically, indirect cues from a prominent predator—*Anoplolepis* ants—were necessary and sufficient to reduce participation in collective prey capture and attack speed during staged foraging events. Furthermore, predator cues, and indirect cues in particular, nullified the well-documented effects of colony personality composition on collective foraging behavior. So, while colony predation rates on *S. dumicola* by *Anoplolepis* ants are high, it appears that *S. dumicola* colonies might also pay an additional price for ants being present in the vicinity of their nest in the form of depressed foraging aggressiveness, and therefore, efficacy (Pinter-Wollman et al., 2017). This further suggests that these ant predators could suppress the positive effects of bold individuals on group success, even if *S. dumicola* colonies are lucky enough not to be subjected to a physical raid, which are typically lethal for the entire spider colony (Henschel, 1998; Keiser et al., 2015b; Wright et al., 2016a).

Given the diversity and abundance of species spanning varying degrees of sociality and complexity, from herding animals to eusocial insect societies, the findings herein could have far-reaching implications. Consistent individual differences in behavior that impact collective outcomes, like those seen in *S. dumicola*, have been discovered in countless animal species such as spiders (Johnson and Sih, 2005), water striders (Sih et al., 1990), ants (Modlmeier et al., 2012), bees (Wray et al., 2011), wasps (Wright et al., 2017a; Wright et al., 2016b), fish (Bell and Sih, 2007), rodents (Daly et al., 1992), birds (Aplin et al., 2014), primates (Flack et al., 2006), and more. For many animals, such variation has proven to be of ecological importance (Jandt, 2013; Modlmeier et al., 2015a; Sih et al., 2004; Sih et al., 2012). The ratios of different personality types within groups often predict group behavior (Pinter-Wollman, 2012), survival and reproductive output (Pruitt, 2013; Pruitt and Goodnight, 2014; Wray et al., 2011), and can be associated with societal efficiency (Chittka and Muller, 2009; Modlmeier et al., 2012; Pruitt and Riechert, 2011a; Waibel et al., 2006; Wright et al., 2014b; Wright et al., 2015). Most, if not all, animals must respond at some time to the threat of predation, and shifts in prey behavior are often used as a first line of defense (Nonacs and Blumstein, 2010). Our findings that predators may disrupt the effects of group composition on group function suggests that the mere presence of predators could negatively impact the performance of a diversity of animal societies.

## Acknowledgements

We would like to thank Mr. Chunky, the rock locust, for being a model citizen to us all. Funding for this research was generously provided by NSF IOS grants 1352705, 1455895 to JNP, 1456010 to NPW, and NIH GM115509 to JNP and NPW.

## Table headers and figure legends:

**Table 1**: Results of the GLMM examining the effects on response to a simulated prey including degrees of freedom (df), chi-square test statistic, and p-values.

**Table 2**: Results of a GLMM examining the changes in number of attackers and latency to attack in the different treatment groups over time.

**Table 3**: Results from 2-Way ANOVAs comparing direct and indirect effects, as well as the interaction between these two modalities.

**Figure 1:** Mean number of spider attackers observed over time in the four predator-exposure treatment groups. Different letters depict significant differences between treatments ($p<0.05$). When no letters are present, treatments do not significantly differ. Error bars show standard error.

**Figure 2:** Mean latency to attack over time in the four predator-exposure treatment groups. Different letters depict significant differences between treatments ($p<0.05$). When no letters are present, treatments do not significantly differ. Error bars show standard error.

**Figure 3:** Mean number of attackers vs the proportion of bold individuals in the group over time for the four predator-exposure treatment groups. P-values indicating the significance of the linear relationship from a regression analysis are noted on each plot.

**Table 1**:

| **Predictor variable** | ***df*** | **χ2** | ***p*-value** |
|---|---|---|---|
| **No. of attackers** | | | |
| Day # | 3 | 90.4 | < 0.0001* |
| Treatment | 3 | 69.7 | < 0.0001* |
| Day # * Treatment | 9 | 30.6 | 0.0003* |
| Whole model | 15 | 165.2 | < 0.0001* |
| | | | |
| **Latency to attack** | | | |
| Day # | 3 | 20.7 | 0.0001* |
| Treatment | 3 | 11.9 | 0.0077* |
| Day # * Treatment | 9 | 10.7 | 0.29 |
| Whole model | 15 | 41.7 | 0.0002* |

**Table 2**:

| | **Number of attackers** | | | **Latency to attack** | | |
|---|---|---|---|---|---|---|
| Independent variable<br>**Treatment** | Indirect | Direct | Indirect + direct | Indirect | Direct | Indirect + direct |
| **Day 0** | | | | | | |
| indirect cues | - | - | - | - | - | - |
| direct cues | 0.96 | - | - | 0.93 | - | - |
| direct + indirect cues | 0.92 | 0.68 | - | 0.9 | 0.99 | - |
| Control (no ants) | 0.99 | 0.94 | 0.94 | 0.88 | 0.99 | 1 |
| **Day 5** | | | | | | |
| indirect cues | - | - | - | - | - | - |
| direct cues | 0.69 | - | - | 0.97 | - | - |
| direct + indirect cues | 0.99 | 0.61 | - | 0.95 | 0.81 | - |
| Control (no ants) | 0.0002* | 0.0088* | 0.0001* | 0.34 | 0.58 | 0.14 |
| **Day 10** | | | | | | |
| indirect cues | - | - | - | - | - | - |
| direct cues | 0.097 | - | - | 0.34 | - | - |
| direct + indirect cues | 0.91 | 0.33 | - | 0.98 | 0.17 | - |
| Control (no ants) | < 0.0001* | 0.0016* | < 0.0001* | 0.45 | 0.012* | 0.68 |
| **Day 15** | | | | | | |
| indirect cues | - | - | - | - | - | - |
| direct cues | 0.62 | - | - | 0.56 | - | - |
| direct + indirect cues | 0.98 | 0.83 | - | 0.67 | 0.99 | - |
| Control (no ants) | < 0.0001* | < 0.0001* | < 0.0001* | 0.98 | 0.34 | 0.44 |

Table 3:

| | Number of attackers | | | Latency to attack | | |
|---|---|---|---|---|---|---|
| **Day # and cue** | *F* Ratio | *p* | LogWorth | *F* Ratio | *p* | LogWorth |
| **Day 0** | | | | | | |
| Direct | 0.0021 | 0.96 | 0.016 | 0.14 | 0.71 | 0.15 |
| Indirect | 0.54 | 0.46 | 0.33 | 0.19 | 0.66 | 0.18 |
| Direct*Indirect | 0.684 | 0.41 | 0.39 | 0.32 | 0.57 | 0.24 |
| **Day 5** | | | | | | |
| Direct | 5.71 | 0.019* | 1.71 | 1.56 | 0.21 | 0.67 |
| Indirect | 15.6 | 0.0002* | 3.77 | 3.27 | 0.074 | 1.13 |
| Direct*Indirect | 4.91 | 0.029* | 1.53 | 0.29 | 0.58 | 0.23 |
| **Day 10** | | | | | | |
| Direct | 4.95 | 0.029* | 1.54 | 3.87 | 0.052 | 1.28 |
| Indirect | 30.6 | < 0.0001* | 6.42 | 0.17 | 0.68 | 0.16 |
| Direct*Indirect | 9.85 | 0.0024* | 2.65 | 6.22 | 0.0146* | 1.83 |
| **Day 15** | | | | | | |
| Direct | 11.1 | 0.0013* | 2.87 | 3.89 | 0.052 | 1.28 |
| Indirect | 25.3 | < 0.0001* | 5.53 | 0.017 | 0.89 | 0.048 |
| Direct*Indirect | 14.8 | 0.0002* | 3.62 | 0.14 | 0.71 | 0.15 |

**Figure 1**:

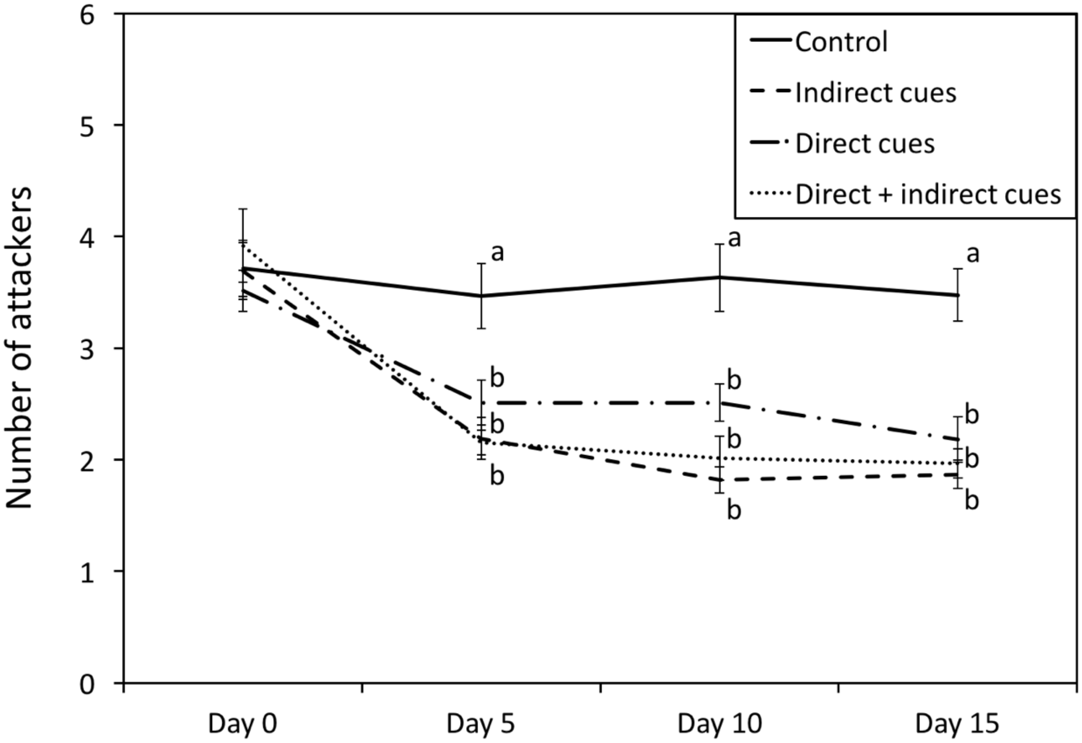

Number of attackers
0
1
2
3
4
5
6
Day 0
Day 5
Day 10
Day 15
Control
Indirect cues
Direct cues
Direct + indirect cues
a
a
a
b
b
b
b
b
b
b
b
b

**Figure 2**:

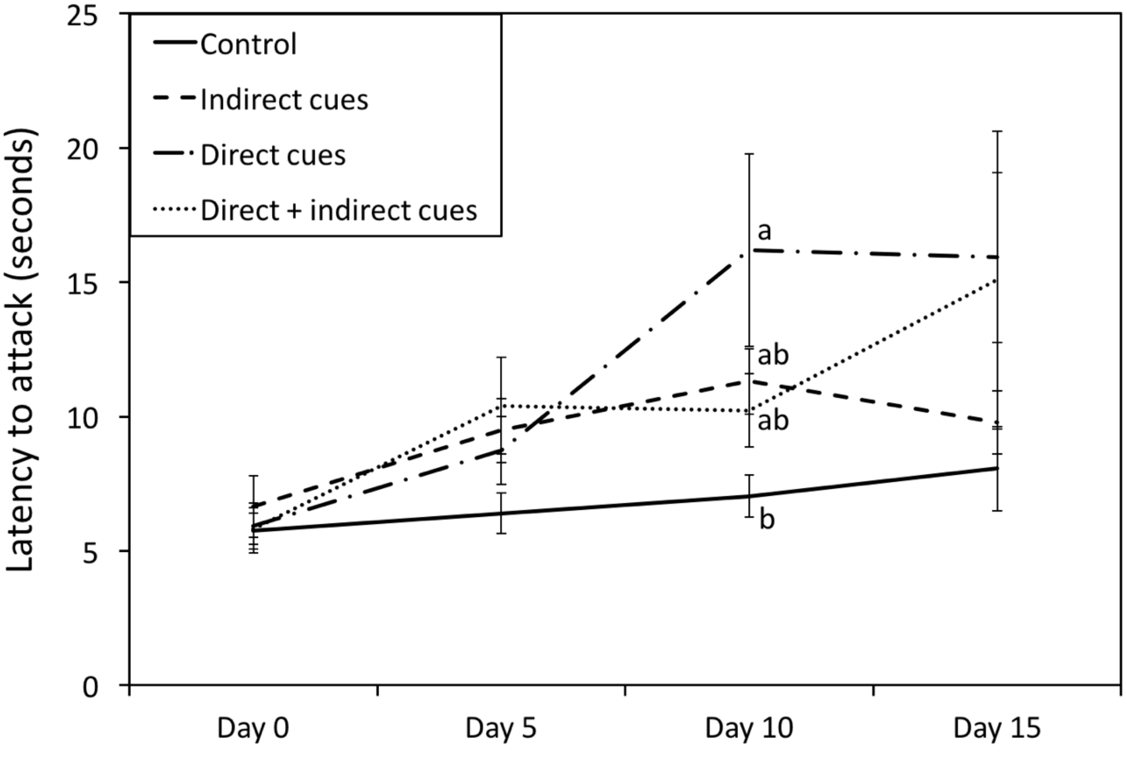
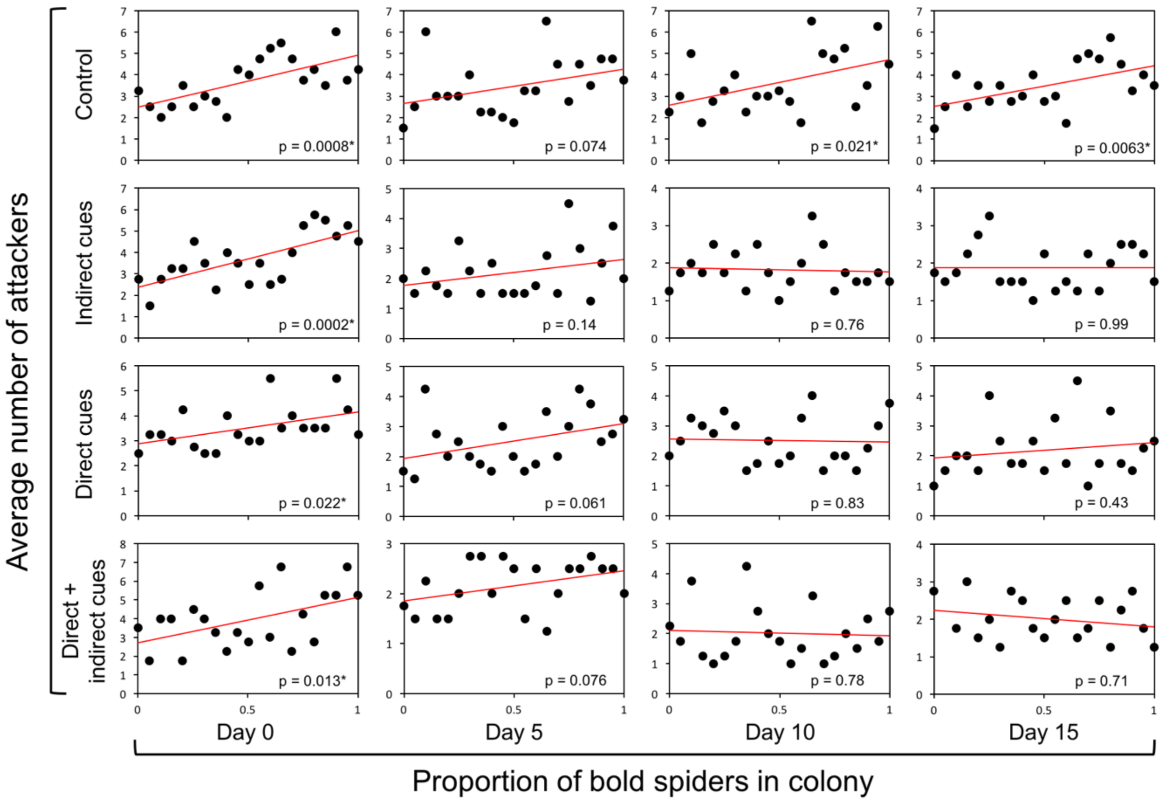

Latency to attack (seconds)
0
5
10
15
20
25
Day 0
Day 5
Day 10
Day 15
Control
Indirect cues
Direct cues
Direct + indirect cues
a
ab
ab
b

**Figure 3:**


Average number of attackers
Control
Indirect cues
Direct cues
Direct + indirect cues
p = 0.0008*
p = 0.074
p = 0.021*
p = 0.0063*
p = 0.0002*
p = 0.14
p = 0.76
p = 0.99
p = 0.022*
p = 0.061
p = 0.83
p = 0.43
p = 0.013*
p = 0.076
p = 0.78
p = 0.71
0
0.5
1
Day 0
Day 5
Day 10
Day 15
Proportion of bold spiders in colony

# III. BOTH GROUP AND IMMIGRANT EXPERIENCE ARE MORE IMPORTANT THAN BEHAVIORAL COMPOSITION IN DETERMINING COLLECTIVE LEARNING

## Abstract

In social animals, individuals can vary in the information they have about their environment. Specifically, information held by the group majority or by socially influential individuals can have a substantial impact on group function. In this study, we examined whether the information about a predatory cue held by a single individual can influence the behavior of a naïve or an experienced group. We created experimental groups of the social spider *Stegodyphus dumicola* that were either iteratively exposed to a dangerous predator, the ant *Anoplopepis custodiens,* or kept in safety. We then seeded these groups with an "immigrant" individual that either had or did not have prior experience with the predator and was either shy or bold. We evaluated colonies' response towards predators over multiple trials to determine the effect of the immigrant's and the majority's prior experience with the predator and the immigrant's boldness. We found that groups adopt a "better safe than sorry" strategy, where groups avoided predators when either the group or the immigrant had been previously exposed to predatory ants, regardless of immigrant boldness. These findings suggest that past experience with predators, even if only by a single individual in the group, can alter the collective learning of societies in a seemingly advantageous manner.

## Introduction

Many animals live in groups, as group living often confers advantages to its constituents (Krause and Ruxton, 2002). The advantages of sociality include increased vigilance toward predators (Lima, 1995; Roberts, 1996), decrease in vulnerability to predators via "dilution effects" (Dehn, 1990; Foster and Treherne, 1981; Hamilton, 1971), increased offspring survival (Silk, 2007), and higher efficiency in foraging and thermoregulation (Clark and Mangel, 1986; Gilbert et al., 2006; Jones and Oldroyd, 2007; Kerth, 2008). A crucial, yet cryptic, benefit of group living is the ability of social groups to acquire wide-ranging information about the current state of their environment by collectively accumulating the narrow experiences of many individuals (Brodbeck and Greitemeyer, 2000; Pacala et al., 1996; Thornton and Clutton-Brock, 2011). Important environmental information, such as the presence of predators and other threats, is often initially picked up by only one or a few individuals. When this information is vital for the longevity and survival of the individuals in the group, the informed individuals often accurately convey the information to others, for example by emitting specific alarm calls (Ferkin et al.; Seyfarth et al., 1980). The information may be further amplified by naïve individuals transmitting the new information to others, or responding appropriately and providing example to others (Chivers and Ferrari, 2015).

Groups can benefit from assimilating the experiences of individuals in many ways. For instance, in elephants, older females (matriarchs) have had more time to accumulate information over their lifetime, such as the location of seldom used water holes (Foley et al., 2008), or the identities of other elephant groups (McComb et al., 2011). This information increases both the survival and reproductive success of herds led by older matriarchs. Group members can garner useful information from individuals via social learning (Thornton and

Clutton-Brock, 2011). Some prominent examples of social learning include the spread of novel behavioral innovations such as tool use (Hobaiter et al., 2014; Pescetta et al., 2008) and food washing (Itani, 1958), as well as novel foraging strategies (Aplin et al., 2015; Heyes and Galef, 1996; Lefebvre, 1995) and learning to avoid unfamiliar predators (Crane et al., 2015; Griffin, 2004). The primary benefit of social learning is that it enables animals to acquire the fitness advantages associated with a behavior without needing to discover it anew or be near the innovator after the behavior is learned. However, these advantages might be impacted by what information is learned and from whom it is learned. For example, groups might receive disparate or conflicting information from different individuals, which then need to be negotiated (Conradt, 2012).

Individuals may possess different, sometimes mutually exclusive, information about their environment and may have different preferred outcomes (Couzin et al., 2005; Dostalkova and Spinka, 2007). For example, individuals could differ in desired food types (Fennessy, 1984; Ruckstuhl and Neuhaus, 2002), hunger level (Krause et al., 1992), and levels of exhaustion (King et al., 2008; Krause et al., 1992). In contrast, some group members may lack relevant information about their environment, such as about the presence of predators or the location of resources (Couzin et al., 2005; List et al., 2009; Sumpter and Pratt, 2009). Successfully negotiating these conflicting levels of information requires information sharing between individuals, and the risk of reaching erroneous decisions tends to decrease as the number of informed decision makers increases (Sumpter and Pratt, 2009). Such information sharing has been extensively studied in the nest selection process of honeybees (Seeley, 2010). Honeybee scouts often discover several new nest locations of varying quality, and each scout conveys both the location and quality of a potential nest site to recruit other workers who will form a preference to a particular site. When a quorum is reached, i.e., nearly everyone in the colony reaches a similar preference to a particular site, the colony will relocate to the new nest (Seeley and Buhrman, 1999). Similar information sharing also takes place for relocating nests in ants (Franks et al., 2009), predator avoidance in fish (Ward et al., 2011; Ward et al., 2008), and finding optimal migration routes in birds (Simons, 2004; Wallraff, 1978). In these cases, individuals appear to have an equal say, and consensus is eventually reached by a majority vote (Krause et al., 2010). But not all animal societies are democracies; in some societies, certain individuals are far more influential than others.

Individuals that wield disproportionate influence on their groups are referred to as "keystone" individuals (Modlmeier et al., 2014d), and they can act as leaders (Stroeymeyt et al., 2011), catalysts (Donahoe et al., 2003), organizers (Robson and Traniello, 2002), tutors (Knoernschild et al., 2010), etc. Given their influence on groups, one might suppose that the consequences of information held by these individuals would be amplified in comparison to similar information held by non-keystones, as in the example of the elephant matriarchs above. When keystones possess accurate information about their environment, this influence should therefore have a large positive effect on group success. However, when keystones possess inaccurate information about their environment, we would expect the ramifications on their groups to be quite costly (Pruitt et al., 2016). In fluid groups, such as those with fission-fusion dynamics, or frequent dispersal, immigrants have the potential to introduce new information that may be different or in conflict with the information possessed by the group majority (Kerth et al., 2006; Sueur et al., 2011). If these immigrants also possess keystone traits, groups may be more susceptible, for better or worse, to their arrival.

The African desert social spider, *Stegodyphus dumicola*, is an emerging model system for the study of highly influential, or “keystone”, individuals (Keiser et al., 2016c; Pruitt and Keiser, 2014a; Pruitt and Pinter-Wollman, 2015; Pruitt et al., 2016). Colonies of up to ~1000 spiders are found in southern Africa, and collectively build dense three-dimensional silken retreats surrounded by multiple two-dimensional capture webs (Seibt and Wickler, 1990). In these spiders, the group’s boldest individual has a disproportionately large influence on colony behavior, such as increasing foraging speed and magnitude, participation in web maintenance, colony mass gain, and altering patterns of disease transmission (Keiser et al., 2016a; Keiser et al., 2016c; Pruitt and Keiser, 2014a; Pruitt et al., 2016). Bold individuals achieve these feats by catalyzing activity within their normally sedentary, shy colony mates. The magnitude of this catalytic effect is directly proportional to the boldness of the boldest individual, as well as to the duration of their presence within the colony (Pruitt and Keiser, 2014a; Pruitt and Pinter-Wollman, 2015). Furthermore, bold individuals can transfer information to other group members. Colonies containing bold individuals with accurate information about their environment learn to attack novel prey stimuli more quickly than colonies without informed, or colonies with misinformed, individuals. Furthermore, colonies containing bold individuals with inaccurate information take longer to attack prey and avoid predators, consequently gaining less weight than other colonies. Thus, keystone individuals can be potentially harmful to colonies when their information about the environment is inaccurate (Pruitt et al., 2016). *S. dumicola* colonies also do not expel or attack foreign conspecifics, or even foreign congeners (Seibt and Wickler, 1988), and colonies in proximity to one another in nature will often fuse, share a capture web, and exchange individuals (Seibt and Wickler, 1988). Along with the arrival of new colony members comes an influx of new individual experiences and information to be exchanged and incorporated. It is therefore plausible that bold “keystone” individuals with inaccurate information about the environment may immigrate into colonies composed of individuals with conflicting accurate information, or *vice versa*. Here we examine how conflicting information is negotiated in this system.

*S. dumicola* colonies are commonly raided by predatory ants (*Anoplolepis custodiens* and *A. steingroveri*), and these raids can be responsible for up to 90% of colony extinction events where the range of the spiders and ants overlap (Henschel, 1998; Keiser et al., 2015b). Spider colonies reduce their speed and magnitude of response to the predatory ants over repeated exposures (Wright et al., 2016a). Furthermore, exposure to predatory ants eliminates the well-studied relationship between colony personality composition and collective behavior, and thus may disrupt keystone and other leader-follower effects observed in *S. dumicola* (Wright et al., 2017b).

In this study, we compare the effects of immigrant and colony information on collective behavior in *S. dumicola*. Specifically, we compare situations where colony experience matches or mismatches the experience of newly introduced immigrant individuals of varying boldness. We ask whether the information held by immigrants takes precedence in determining colonies’ response towards both dangerous predators and innocuous prey, and whether immigrant personality (bold vs. shy) plays a role in this dynamic. To do this, we created experimental colonies that varied their experience with predators, and added to them immigrants of varying boldness and varying experience with predators. We test the following hypotheses: (1) the *democratic hypothesis*: colonies will behave according to the information possessed by the majority of individuals; (2) the *dictator hypothesis*: colonies will behave in accordance with the experience of influential keystone immigrants; (3) the *better safe than sorry hypothesis*:

colonies will behave in a manner that mitigates overall risk and respond with caution if either the immigrant or colony has experience with predators, regardless of immigrant keystone status.

## Methods

### *Colony collection and behavioral assays*

Colonies of *S. dumicola* were collected from fences and bushes around Upington in the Northern Cape of South Africa, and brought into the lab the same day. Each spider was individually isolated from its nest mates in small 30ml plastic condiment containers. We then measured each spider's boldness by placing them into a larger arena, allowing them to acclimate to the new container for 60s, and administering two gentle puffs of air to their anterior prosoma using a rubber squeeze-bulb. These air puffs resemble an attack from an avian predator, causing the spider to cease activity and pull its legs in against their body in a "huddle" position (Lohrey et al., 2009; Pruitt et al., 2013; Riechert and Hedrick, 1990). The latency to unhuddle and move one whole body length following these air puffs is our measure of boldness. Boldness is defined as the propensity of an individual to engage in risky behavior (Sloan Wilson et al., 1994) and resuming normal activity quickly after interacting with a possible predator (air puffs) is here deemed risky or "bold" behavior. These latencies scores are then subtracted from 600 (the maximum value) so that higher numbers reflect greater boldness scores. Spiders with intermediate boldness values were not used in the present study. We used maximally shy spiders for our colony constituents and for the shy immigrants (i.e., spiders that never unhuddled during boldness trials and had a boldness score of zero). Bold immigrants all had latencies to resume movement under 60s (i.e., boldness scores greater than 540).

### *Colony creation*

Following individual boldness trials, we constructed 80 experimental colonies containing 9 shy spiders each. Each colony was housed in a separate 250ml clear, plastic parfait cup containing a few twigs of acacia hookbush (*Acacia mellifera*) for the spiders to use as nesting substrate. One bold or shy future "immigrant" spider from the same source colony was kept separately in a 30ml plastic condiment cup until its addition to the 9-individual colony after 7 days. Each experimental colony, and its respective immigrant, was derived from a single source colony from an area where ants were not abundant, and spiders from different source colonies were never combined so that within-group relatedness and familiarity was maintained (Laskowski et al., 2016a; Laskowski and Pruitt, 2014b; Modlmeier et al., 2014e). Half of the experimental colonies (N = 40) were exposed to predatory *A. custodiens* ant workers twice a day for 7 days prior to immigrant additions (ant+ colonies treatment), and the other 40 colonies were not exposed to ants prior to immigrant additions (ant- colonies treatment). Details of ant exposures are outlined below. Within each of the above groups, half (20) of the colonies received a bold immigrant and the other half a shy immigrant. Half of the immigrants in each of these groups were pre-exposed to predatory ant cues (ant+ immigrants treatment), and the other half were not (ant- immigrants treatment). Thus, we established 8 treatments in total, 10 replicates in each, which were deployed in a fully factorial 2 × 2 × 2 design: colony experience (ant presence +/-), immigrant experience (ant presence +/-), and immigrant personality (shy/bold).

### *Immigrant Predator Exposure Treatments*

Following individual boldness trials, we exposed half of the future immigrants to predatory ants (ant+ immigrants treatment). We punctured small holes in the bottom of the 30ml container of the spider and nested it within another identical cup with two predatory ants that were free to move around in the space between the bottoms of the stacked cups. We kept spiders in this set up for 7 days and dead ants were replaced with live ones immediately when discovered. This set up allowed any ant cues to permeate to the spiders without direct contact. *S. dumicola* respond to these cues by decreasing their foraging activity and increasing their latency to attack ants that encounter their webs (Wright et al., 2017b). The other half of the immigrant spiders (ant- immigrants treatment) experienced an identical procedural control treatment in which the chamber between the two cups was free of ants.

### *Colony Predator Exposure Treatments*

To expose colonies to predator cues we followed a similar procedure to the one for the isolated immigrants. We punctured small holes in the bottom of the containers of the experimental colonies and nested them within other identical cups. To half of the experimental colonies (ant+ colonies treatment) we added 5 *A. custodiens* workers to the space between the nested cups for 7 days. In addition to ants being placed beneath the colonies, each ant+ colony was exposed directly to ants twice daily, 6 hours apart, over the course of the same 7-day period. In each direct exposure, we placed a single *A. custodiens* worker in the capture web and allowed the spiders to briefly interact with the ant. Ants were removed after we observed spiders interacting with them so that the colonies were unable to consume the ants to keep feeding regimes constant across all treatments.

We tested each ant+ colony for their initial aggressiveness and defensive behavior toward ants by placing a single *A. custodiens* worker in the center of the colony's capture web and measuring colonies' latency to attack the ant and the number of attackers that responded. This was a separate occasion from the daily ant "exposures." We also recorded the number of spiders that were observed spinning cribellate silk every 2 minutes over a 10-minute period (5 scan samples per trial). Cribellate silk is a particularly tangly type of silk these spiders produce defensively when exposed to predatory ants to line their capture webs and impede the advancement of ants into their vulnerable retreats (Henschel, 1998). The two trials of direct exposure to ants on the first day were averaged to obtain an estimate of initial colony aggressiveness and defensive behavior.

### *Impact of experience on collective response*

After the 7 days of ant exposures to the ant+ colonies and immigrants, the bold and shy immigrants previously set aside were added to colonies that either matched or mismatched their own experience. To determine whether and to what degree immigrant boldness, or previous experience with predators, shapes collective behavior, colonies were tested twice a day, for 5 days following immigrant additions, for aggressiveness toward innocuous (paper) prey (details below), and once a day for aggressiveness and defensive cribellate spinning behavior toward a dangerous (ant) predator (as detailed above). See Supplementary Table S1 for a visual breakdown of the experimental timeline.

### *Collective attack of prey*

To evaluate each colony's initial aggressiveness towards innocuous prey, we tested the colonies containing 9 shy spiders prior to the 7 days of ant exposure treatments 4 times in a 24-hour period (each 4 hours apart). These baseline aggressiveness assays were performed to uncover how colonies initially responded to prey before treatments were administrated. This was initiated by placing a 1×1cm piece of paper (representing an innocuous prey item) in the center of the capture web and vibrating the paper with a small handheld vibrator. This causes the paper to flutter, resembling the vibrations that a small winged insect might make whilst struggling in the capture web. We recorded the latency for the first spider to attack - make physical contact with the paper and the number of spiders that were recruited to the capture web during the attack sequence. These measures give us an estimate of both the speed and magnitude of an attack. All 4 trials were then averaged to get an estimate of average colony aggressiveness. On the day following the baseline aggressiveness trials to innocuous prey, we initiated our ant exposure (+/-) treatment colonies described above.

### *Statistical methods*

We analyzed this experiment as a 2×2×2 fully factorial design using ANOVAs with colony experience (predators +/-), immigrant experience (predators +/-), immigrant personality type (bold/shy), and their interactions as independent variables and either response to prey or response to predator (latency to attack, # of attackers, and defensive cribellate silk spinning) on each of the 5 days as the dependent variables. To correct for multiple testing (two ANOVAs at each of five time points = 10 time points total), we used a conservatively Bonferroni-modified $\alpha$ of 0.005.

## Results

*Colony Response Towards a Dangerous Predator (ants)*

**Colony experience**: Exposure to predators decreased aggressiveness towards them over time. Unexposed colonies were faster to attack ants in the capture web than predator-exposed colonies early on (~850% faster on day 1 ($p < 0.0001$), ~300% faster on Day 2 ($p < 0.0001$), and ~230% faster on Day 3 ($p = 0.0004$)) (Figure 1A & 1B). Unexposed colonies also initially deployed more attackers than exposed colonies (~240% more on day 1 ($p < 0.0001$), ~260% more on day 2 ($p < 0.0001$), and ~240% more on day 3 ($p = 0.0025$) (Figure 1C & 1D). Colony experience had no influence on the number of defensive cribellate silk spinners observed (Table 1).

**Immigrant experience**: Unexposed colonies that received predator-experienced immigrants displayed similar attack latencies to those of unexposed colonies that received unexperienced immigrants in days 1-3. However, unexposed colonies that received experienced immigrants dramatically increased their latency to attack ants by over 200%, to resemble attack latencies comparable to those of exposed colonies, by days 4 and 5 (Day 4: p = 0.0012; Day 5: p = 0.0036), while attack latencies of unexposed colonies that received unexperienced immigrants did not exhibit a similar shift (Figure 1A & 1B). A nearly identical pattern emerged for the number of attackers deployed: early on (days 1-3) there were no differences between unexposed colonies that received experienced immigrants and unexposed colonies that received unexperienced immigrants. However, a shift occurred on day 4, when unexposed colonies that received experienced immigrants radically decreased the number of attackers to resemble attack numbers of exposed colonies (Figure 1C & 1D). The delayed effect of immigrant experience on colony behavior suggests that a combination of personal and socially obtained information is necessary to detect a colony level response, or that it takes time for social information to spread through the group. Immigrant experience, however, had no influence on the number of defensive cribellate silk spinners observed.

*Colony Response Towards Innocuous Prey (paper)*

**Colony experience**: Exposure to predators had no observable influence on colonies' latency to attack or on the number of attackers deployed to an innocuous prey stimulus.

**Immigrant experience**: The number of attackers that responded to innocuous prey depended on the boldness of the immigrant. Immigrant boldness had increasingly stronger catalyzing effects on group foraging as the experiment went on, with bold immigrants ultimately increasing colony foraging on innocuous prey by 46% on average on day 5, regardless of whether the immigrant or the colony had been exposed to predators ($p < 0.0001$). All four treatment groups with bold immigrants deployed more foragers than all four treatment groups with shy immigrants on days 3 and 5, and most treatments with bold immigrants deployed more attackers than colonies with shy immigrant treatments on the other days as well (Table 1). We did not detect a difference among any of the treatments in latency to respond to prey at any time point.

## Discussion

Our results support the '*better safe than sorry*' hypothesis by demonstrating that information content, rather than majority experience or the experience of highly influential "keystone" immigrants, takes precedence in determining collective behavior in *S. dumicola* colonies when that information signals risk. Specifically, immigrants that had previous experience with predator cues caused unexposed colonies to dramatically reduce their speed of response to ants by 200%, and the number of attackers on ants by nearly 400%, ultimately yielding attack speeds and numbers indistinguishable from those of previously exposed colonies (Figure 1A). Immigrant personality (bold vs. shy), which reflects their status as a keystone (Pruitt et al., 2013), had no influence on response to dangerous ants. For innocuous prey (paper), we did not find any relationship between immigrant experience and collective behavior. We did however find a strong positive relationship between immigrant boldness and the number of attackers deployed to innocuous (but not dangerous) prey, which is corroborative of the keystone dynamics that have been described previously in this system. Thus, we found no evidence that colonies preferentially base collective decisions on majority information or on immigrant keystone status, and therefore we reject both the *democracy hypothesis* and the *dictator hypothesis*. Colonies, however, remained cautious when constituents had prior experience with predators and quickly became more cautious when immigrants with prior predator experience were introduced to unexposed colonies. This result supports the *better safe than sorry hypothesis*, where colonies act based on information alone to mitigate risk.

Our results demonstrate high levels of behavioral plasticity in *S. dumicola* colonies, where groups can modify their behavior quickly in response to useful information regarding risk. The presence of behavioral plasticity in *S. dumicola* is not entirely surprising, as several studies have shown high levels of behavioral plasticity in this species in other contexts, such as in foraging and defensive cribellate silk spinning behavior (Wright et al., 2016a; Wright et al., 2017b). However, this plasticity has always been linked to the collective personalities of the groups, or the personality of "keystone" individuals due to their ability to alter the collective behavior of groups containing shy individuals (Pruitt et al., 2013; Pruitt and Keiser, 2014a). The present study differs from these in its focus on information and personality rather than personality per se, and demonstrates that information can override majority experience and personality effects when the information is pertinent for colony survival. A past study on how colonies deal with keystone information/misinformation demonstrated that colonies are less susceptible to mistakes when responding to predators vs. innocuous prey (Pruitt et al., 2016), perhaps mirroring the cautious behavior revealed in this study. The ability of uninformed colonies to quickly shift their behavioral phenotypes to match those of informed colonies hints at a long evolutionary history with predatory ants, and at the possible benefits of being forewarned to their presence (Henschel, 1998; Keiser et al., 2015b). Colonies thus appear to adopt a "better safe than sorry" strategy. This is likely because preparing for an ant raid that never comes (false positive) is considerably less costly than failing to adequately prepare when a raid occurs (false negative), especially when raids are common and typically result in total colony annihilation (Keiser et al., 2015b; Wright et al., 2016a).

While our results suggest that the immigrants can transmit information regarding their past experience to their new nest mates, the mechanism of this information transfer is unknown. It is unlikely that colonies are responding to ant cues that have hitchhiked onto the immigrants, because immigrant additions coincide with exposure to ants in this study. Additional control groups using exposed and unexposed plastic bead "immigrants" would have been useful to fully flesh out these details. Another possible mechanism for information dissemination includes leader-follower dynamics that are commonly described in this species in the context of “keystone” individuals (Grinsted et al., 2013; Pruitt et al., 2013; Pruitt and Keiser, 2014a; Pruitt et al., 2016). While keystones in this species usually refer to spiders with a bold behavioral type, this study highlights the fact that bold individuals are not the only kinds of individuals to wield situational influence. In environments where predatory ants are absent, or at tolerably low abundance, keystone boldness may be more important in of augmenting colony foraging rather than responding to seldom encountered predators. However, when predatory ants are abundant, as simulated by the repeated exposures to the ants that we performed, individual-level traits, like boldness, appear far less important in shaping colony collective behavior than acquired information about the predator.

Keystone effects of bold immigrants on foraging on innocuous prey were retained in all treatments, regardless of whether the colonies or the immigrants had been previously exposed to predators. This retention of keystone effects was not expected, as a previous study (Ferkin et al.) had shown that exposure to predators appeared to over-ride the link between colony personality composition and collective foraging on innocuous prey. In the previous study, groups containing a higher proportion of bold individuals attacked innocuous prey in larger numbers than those containing more shy spiders. However, this positive relationship between the proportion of bold individuals and attack magnitude vanished when colonies were exposed to predatory ants as in the present study. Given that the addition of bold keystones to shy colonies alters colony composition, it was thought likely that predator presence could potentially nullify keystone effects (Wright et al., 2017b). Apparently, keystone effects can be retained and be up- or down-regulated in a context-specific manner, depending on perceived levels of threat. An important difference between Wright et al (2017b) and the present study is that colonies in the previous study did not receive added keystones/immigrants and were larger (20 individuals vs 10 here). Instead, colonies maintained their compositions throughout the study during predator exposures while being repeatedly tested for group foraging on innocuous prey. The addition of outside individuals to otherwise stable groups appears to be a necessary condition to both augment (in the case of bold "keystones") or curtail (in the case of forewarned immigrants) group foraging in a context-specific manner.

An often-overlooked aspect of social living is the potential for acquiring information about the environment via immigrants (Aparicio et al., 2007; Galef and Laland, 2005; Laland and Williams, 1998). In many animal societies, the willingness to leave and join groups can often be tightly linked with animal personality (Cote et al., 2010; Pruitt et al., 2012a), and personality can further dictate the roles that individuals play within their societies (Grinsted et al., 2013; Holbrook et al., 2014; Wright et al., 2014b), as well as their degree of social influence (Modlmeier et al., 2014d; Pruitt and Keiser, 2014a). These properties, in turn, create situations where the mixture of behavioral types within groups can change the collective behavior and success of groups. Nowhere is this property more impressive than in cases where singleton individuals come to wield a disproportionately large influence over their societies (Modlmeier et al., 2014d). However, such immigrants can be advantageous, harmful, or otherwise influential for reasons that transcend innate behavior, such as when one comes to possess important information about the state of the environment. When the information transmitted between individuals in a group is inaccurate or suboptimal, maladaptive traits can sometimes spread throughout a group (Laland and Williams, 1998; Pruitt et al., 2016). However, if a threat is both constant and severe, as is the case with *Anoplolepis* ants to *S. dumicola* colonies, responding to uncertain information may be less costly than doubt when the stakes are high.

## Conclusion

Our data suggest that the experience of bold immigrant individuals is insufficient to outweigh the personal experiences of an entire colony: colonies forewarned about predators do not reverse their cautious behavior tendencies merely because an unexposed bold individual arrives. Moreover, in situations where we detected an effect of immigrant information on colony behavior, bold immigrants appeared to be no more influential than their shy counterparts. Forewarned immigrants, regardless of their personality, accelerated the rate at which naive colonies altered their behavior in response to interactions with predatory ants. This finding suggests that in certain situations, such as being under predator attack, the effect of colony experience and individual history can outweigh the effects of personality-dependent social influence. Colonies disregard the majority opinion and keystone influence in favor of a *better safe than sorry* strategy to mitigate risk. Our results show that *S. dumicola* colonies respond to their environment, and begin to tease apart when certain kinds of individuals (e.g., particular personality types) are likely to be influential, and when they are not. Future experiments will aim to more finely manipulate the proportion of colony members that have experienced predators and the personality types of the individuals with and without predator exposure.

## Acknowledgements

We would like to thank the Tramonto Lodge in Upington, South Africa for providing us with laboratory space for this experiment. Funding for this research was generously provided by NSF IOS grants 1352705/1455895 to JNP, 1456010/1708455 to NPW, and NIH GM115509 to JNP and NPW.

**Table headers and figure legends:**

**Table 1:** P-values of the ANOVA tests for our 2×2×2 fully factorial design for each of the 5 days.

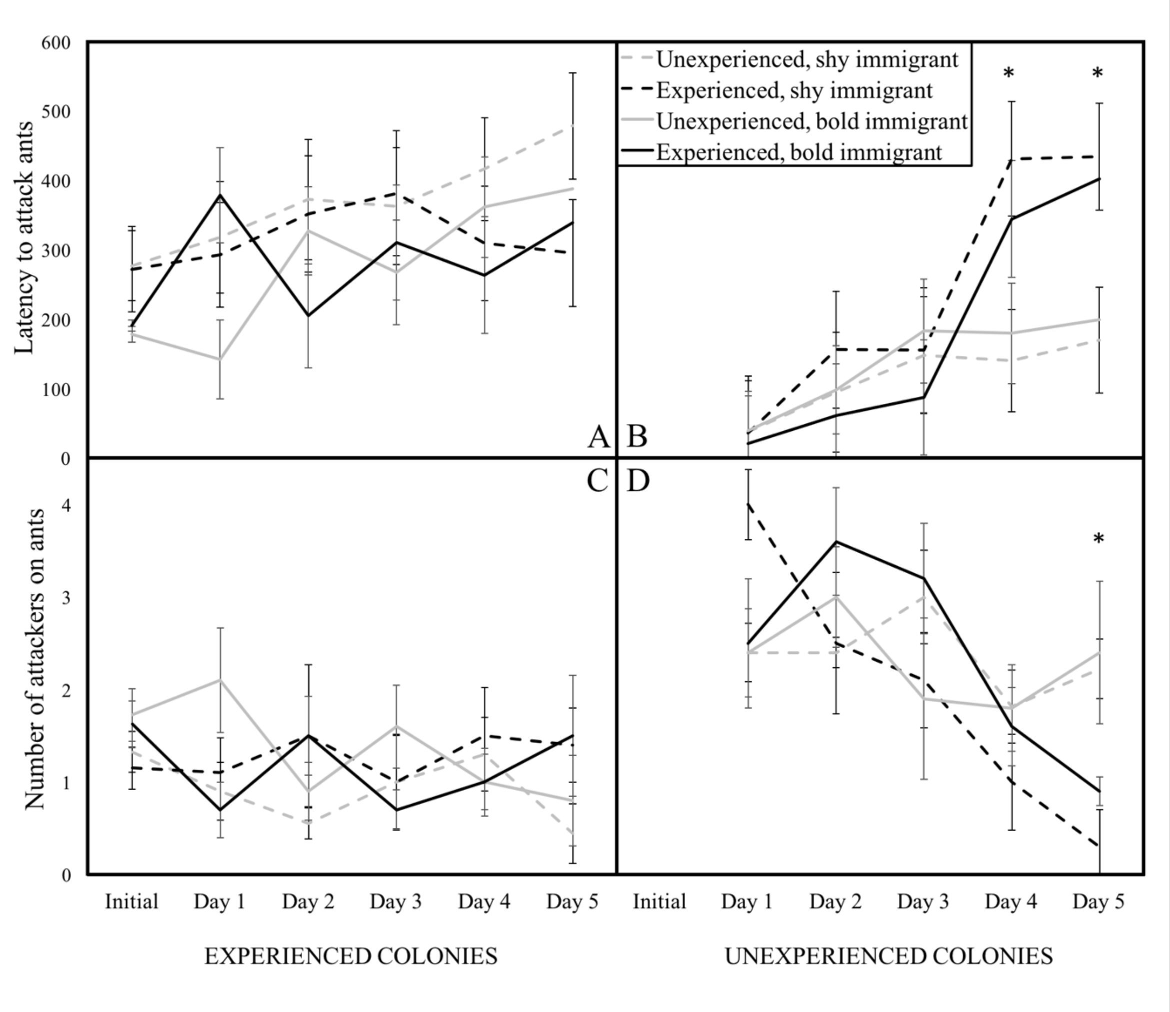
**Figure 1**: Colony collective responses over time. Latency to attack ants (dangerous prey) over time when colonies were (**A**) previously exposed to ants or (**B**) not previously exposed to ants. Latency to attack paper (innocuous prey) over time when (**C**) colonies were previously exposed to ants and (**D**) not previously exposed to ants. Immigrants added to colonies on day 1 differed in predator experience (experienced = red; unexperienced = green) and personality (bold = solid; shy = dashed). Asterisks indicate statistically significant differences between treatments ($p<0.005$).

**Table 1**:

| | Day 1 | Day 2 | Day 3 | Day 4 | Day 5 |
|---|---|---|---|---|---|
| **Latency to attack innocuous prey** | | | | | |
| Immigrant BT | 0.6129 | 0.6438 | 0.9345 | 0.3273 | 0.9253 |
| Immigrant exp. | 0.6664 | 0.4592 | 0.3647 | 0.758 | 0.7915 |
| Colony exp. | 0.6546 | 0.7689 | 0.5403 | 0.7975 | 0.0942 |
| Colony exp.*Immigrant BT | 0.661 | 0.2681 | 0.1703 | 0.3176 | 0.3939 |
| Immigrant exp.*Immigrant BT | 0.7668 | 0.6293 | 0.5386 | 0.6731 | 0.6277 |
| Colony exp.*Immigrant exp. | 0.5151 | 0.5324 | 0.6934 | 0.7441 | 0.5912 |
| Colony exp.*Immigrant exp.*Immigrant BT | 0.7422 | 0.3854 | 0.1433 | 0.9083 | 0.2116 |
| **Latency to attack dangerous prey** | | | | | |
| Immigrant BT | 0.5169 | 0.1428 | 0.273 | 0.4944 | 0.8328 |
| Immigrant exp. | 0.2302 | 0.5358 | 0.775 | 0.5763 | 0.3106 |
| Colony exp. | **<.0001** | **<.0001** | **0.0004** | 0.3063 | 0.21 |
| Immigrant exp.*Immigrant BT | 0.125 | 0.3 | 0.8299 | 0.9724 | 0.7534 |
| Colony exp.*Immigrant BT | 0.6263 | 0.6004 | 0.4314 | 0.89 | 0.8469 |
| Colony exp.*Immigrant exp. | 0.1456 | 0.3873 | 0.5782 | **0.0012** | **0.0036** |
| Colony exp.*Immigrant exp.*Immigrant BT | 0.0827 | 0.988 | 0.4492 | 0.3042 | 0.3981 |
| **No. of attackers to innocuous prey** | | | | | |
| Immigrant BT | 1 | **0.0038** | **0.0007** | 0.0455 | **<.0001** |
| Immigrant exp. | 0.3336 | **0.0054** | 0.0121 | 0.393 | 0.8116 |
| Colony exp. | 0.7465 | 0.2656 | 0.8308 | 0.6203 | 0.8116 |
| Immigrant exp.*Immigrant BT | 0.8716 | 0.0655 | 0.3939 | 0.5584 | 0.6681 |
| Colony exp.*Immigrant BT | 0.2599 | 0.3857 | 0.0906 | 0.0986 | 0.2357 |
| Colony exp.*Immigrant exp. | 0.8716 | 0.8038 | 0.3378 | 0.8924 | 0.2749 |
| Colony exp.*Immigrant exp.*Immigrant BT | 0.7465 | 0.3219 | 0.9149 | 0.226 | 0.1696 |
| **No. of attackers to dangerous prey** | | | | | |
| Immigrant BT | 0.6241 | 0.2048 | 0.9491 | 0.873 | 0.404 |
| Immigrant exp. | 0.7262 | 0.1644 | 0.7497 | 1 | 0.2331 |
| Colony exp. | **<.0001** | **<.0001** | **0.0025** | 0.153 | 0.2572 |
| Immigrant exp.*Immigrant BT | 0.0326 | 0.9227 | 0.8481 | 0.7492 | 0.91 |
| Colony exp.*Immigrant BT | 0.1103 | 0.399 | 0.6552 | 0.425 | 0.827 |
| Colony exp.*Immigrant exp. | 0.0451 | 0.5988 | 0.2798 | 0.1129 | **0.0009** |
| Colony exp.*Immigrant exp.*Immigrant BT | 0.9441 | 0.5988 | 0.1827 | 0.2033 | 0.6459 |

| | | | | | |
|---|---|---|---|---|---|
| **No. of defensive cribellate spinners** | | | | | |
| Immigrant BT | 0.3216 | 0.0334 | 0.7343 | 0.2151 | 0.9103 |
| Immigrant exp. | 0.8809 | 0.7954 | 0.0822 | 0.4272 | 0.6186 |
| Colony exp. | 0.6929 | 0.8492 | 0.2342 | 0.7075 | 0.1017 |
| Immigrant exp.*Immigrant BT | 0.6145 | 0.2489 | 0.5456 | 0.9641 | 0.7589 |
| Colony exp.*Immigrant BT | 0.6337 | 0.278 | 0.5456 | 0.5191 | 0.3125 |
| Colony exp.*Immigrant exp. | 0.9457 | 0.278 | 0.8019 | 0.1941 | 0.3537 |
| Colony exp.*Immigrant exp.*Immigrant BT | 0.9024 | 0.9311 | 0.1551 | 0.3611 | **0.0083** |

**Figure 1:**


600
500
400
300
200
100
0
Latency to attack ants
Unexperienced, shy immigrant
Experienced, shy immigrant
Unexperienced, bold immigrant
Experienced, bold immigrant
*
*
A
B
C
D
4
3
2
1
0
Number of attackers on ants
*
Initial
Day 1
Day 2
Day 3
Day 4
Day 5
Initial
Day 1
Day 2
Day 3
Day 4
Day 5
EXPERIENCED COLONIES
UNEXPERIENCED COLONIES

# GENERAL DISCUSSION

The series of experiments presented herein address an important aspect of collective personality that has yet to be addressed empirically: how the behavioral distribution of colony constituents influences collective behavior in the context of colony defense, how prolonged exposure to predators feeds back to determine the collective behavior of groups, and how groups prioritize information regarding predator presence when that information is possessed by the majority, or singleton immigrants that vary in leadership traits.

Chapter 1 revealed the importance of group composition in determining the magnitude of their defensive response when attacked by deadly social predators. In all previous studies on collective behavior in *S. dumicola*, bold colonies appeared to outperform shy compositions in every measured collective trait, such as prey capture and web repair. Our finding that mixed compositions exhibited twice as much defensive behavior as other compositions helps explain the near ubiquity of of mixed compositions in nature. In Chapter 2, we saw that prolonged exposure to predators, either directly or indirectly, is sufficient to cut colony attack speeds and numbers in response to all prey stimuli in half. And furthermore, exposure to predators effectively erased the well-documented link between colony personality composition and aggressiveness during prey capture. Chapter 3 addressed the question of how groups use information about environmental risk when that information is possessed by singleton immigrants of contrasting behavioral types, or the group majority. This study found that colonies operate on a "better-safe-than-sorry" strategy, and groups rapidly exhibit cautious foraging behavior when either the group or immigrant had previously been exposed to predators, regardless of immigrant behavioral type.

These experiments, both in alone and in combination, reveal a complex relationship between collective personality and predation risk. While these studies further enhance our understanding of ecology of *S. dumicola*, they further demonstrate that the behavior exhibited by a group at any one time is a combination of both internal (group composition) and external (predator presence/absence) factors that may represent a tradeoff between prey capture efficiency and vulnerability to predators. Given the ubiquity of predation as a strong selective force for the vast majority of taxa, social or otherwise, the generalizability of these results cannot be understated. It is my hope that other ecologists will use these findings to better understand the role that fear might play in shaping the collective behavior of their focal systems.

# IV. COLLECTIVE PERSONALITY: WHAT WE DO AND DO NOT YET KNOW

## Introduction

If you have ever had the misfortune of being swarmed by bees or wasps, or have witnessed ants or termites angrily emerge, *en masse*, from underground tunnels in response to your disturbance, then you have observed, or perhaps directly experienced, a type of collective behavior. And, if you repeatedly antagonize many colonies and pay close enough attention, you might notice that colonies often differ consistently in how they respond to your meddling. That is to say, different colonies exhibit distinct "personalities." But while societal traits like aggressiveness in response to a threat may be the most readily observable and conspicuous, there are many other ways that colonies can differ behaviorally that is relevant to their functioning and survival. For instance, individual societies may also differ in how broadly they explore and forage, how well they attend to their young, how finely they divide their labor among tasks, or how they build or excavate complex 3-dimensional nest structures, to name only a few.

In this review article we look back at the last five years of research aimed at exploring the presence and consequences of collective personality, and then provide a roadmap for where this field might go next. Approximately five years ago, Jandt et al. (2014) and Bengston and Jandt (2014a) produced a pair of expansive and exhaustive reviews of the literature on this topic, which have since inspired more than 100 descendant papers. Model taxa for these investigations have included some vertebrates (e.g., birds, fish), however, the majority of studies have used social arthropods for their investigations. Here we aim to summarize earlier work, comment on the field's progress since the 2014 reviews, and compare and contrast the findings gleaned from the field's most prominent model systems (i.e., social spiders and eusocial insects). We then provide the reader with a variety of new hypotheses regarding how collective personality might interact with several other fields of study, including colony life history and performance, population and community ecology.

## What is collective personality?

Personality, which is a property of a population or group, is defined as the presence of temporally consistent behavioral differences between individuals (Sih et al., 2004; Sih et al., 2012). The aggregate is said to have personality, while each individual comprising the aggregate is said to possess a particular "behavioral type" or BT or sometimes "personality type" (e.g., docile vs. aggressive individuals). However, the term "individual" can apply both to individual organisms as well as cohesive social groups (Jandt, 2013). This is particularly relevant in eusocial insects, where colonies can be viewed as extended phenotypes of the queen, and the queen + workers as a type of "superorganism" (Hölldobler and Wilson, 2009). But individuality can apply to other cooperative social groups as well, such as social arachnids and other non-arthropods. And thus, "collective personality" refers to the presence of temporally consistent behavioral differences exhibited between distinct social groups (Bengston and Jandt, 2014b; Jandt, 2013; Jandt and Gordon, 2016).

## How does collective personality arise?

One of the central question to those studying collective personalities, after the near-ubiquity of this phenomenon had been thoroughly documented, has been to understand the mechanisms that give rise to both intra- and inter-group variation in behavioral types and therefore personality. Concerning the origin of colony personality, explanations fall within three, non-mutually exclusive and oft intertwined, categories of influence: genetics, physiology, and environment.

***Genetics***. The queens of eusocial insects can be either inseminated by one or multiple males (Kronauer et al., 2004; Strassmann, 2001). And, this tends to vary widely among species, as well as within certain species (Cole, 1983; Strassmann, 2001). The more males a queen mates with, the more genetically diverse her workers will be, which will result in the expression of a variety of genetic-based behavioral tendencies. In honey bees, for instance, genes affect worker learning ability (Chandra et al., 2000), foraging propensity and preference (Page et al., 1998; Page and Robinson, 1991), defensive behavior (Breed et al., 2004), as well as division of labor (Page et al., 1998; Page and Robinson, 1991; Robinson, 1989). However, species where queens only mate once, and are thus less genetically diverse, still give rise to behaviorally diverse societies (Dornhaus et al., 2008; Jandt and Dornhaus, 2009; Jandt et al., 2009). Genetic variation both within and between queens, then, is thought to contribute to the emergence of individual- and colony-level personality. However, personality variation can also arise in genetically curbed social taxa, such as most social spiders (Holbrook et al., 2014; Pruitt and Riechert, 2011a; Wright et al., 2014b; Wright et al., 2015). Personality in social spiders can arise due to differences in gene expression (Ben-Shahar et al., 2002; Ingram et al., 2005; Rittschof, 2017; Zayed and Robinson, 2012), which can be influenced by a multitude of factors such as individual or colony experience (Niemela et al., 2012; Rittschof, 2017), nutrition (Ament et al., 2008; Ament et al., 2010; Toth and Robinson, 2005; Wheeler et al., 2006), social environment (Beshers et al., 2001; Huang and Robinson, 1996), or age (Beshers et al., 2001; Robinson and Ben-Shahar, 2002; Sullivan et al., 2000). Also, discrete colony-level social polymorphisms can be the result of strong genetic control, such as in the fire ant *Solenopsis invicta*, where worker tolerance of polygyny as well as nest initiation behavior rests on a single locus polymorphism (Keller and Ross, 1998; Ross and Keller, 2002; Wang et al., 2013). Special consideration should be given to the traits of singularly influential individuals, such as queens or other colony initiators, that may influence the behavioral makeup of their future workforce (Doering and Pratt, 2016; Wright et al., 2016b) and, in turn, the collective behavioral tendency of the group. It is important to note that genetic underpinnings of collective personality are indeed *required* for there to be an effective response to selection on inter-group variation. But the transmission of colony-level phenotypes has rarely been demonstrated (Pruitt and Goodnight, 2014; Pruitt et al., 2017a), even circumstantially (Gordon, 2013b).

***Physiology***. As individuals age, many physiological changes occur that can often lead to changes in their behavior. In social insects, the best example of this is the age-related division of labor seen in honeybees known as temporal polyethism (Seeley, 1982). Newly eclosed workers tend to remain inside the colony as nurses, but after several weeks take on more complex foraging duties outside the colony. Changes in the patterns of brain gene expression co-occur during this transition. Thus, variation in age demographics between colonies can contribute to the expression of colony-level phenotypes. Many behavioral differences also arise due to individuals producing different levels of certain hormones. One well-studied example is juvenile hormone (JH), which has been linked with aggressiveness (Pearce et al., 2001; Tibbetts and Huang, 2010), dominance behavior (Barth et al., 1975; Tibbetts and Huang, 2010), behavioral development (Fahrbach and Robinson, 1996; Sullivan et al., 2000), division of labor (Schulz et al., 2002), and reproductive behavior (Barth et al., 1975; Riddiford, 2012). Other factors that can influence physiology and, subsequently, behavior, include diet and nutrition, and even fat content (corpulence) (Blanchard et al., 2000). Variation in any of the above physiological features in group constituents or the emergent physiology of the colony can conceivably shape the way an individual colony will behave.

***Environment***. Often times different collective behaviors are the result of external (i.e. environmental) factors rather than internal (i.e. genetics and physiology) factors (Bengston and Jandt, 2014b). And, these environmental factors can be both biotic and abiotic in nature. For instance, the location of a colony can determine how much light a colony is exposed to, its internal temperature, humidity, maximum size, and nest architecture. Many of these elements have been shown to directly influence colony-level behavior (Dornhaus et al., 2012; Gordon, 1996; Gordon et al., 2013; Gordon et al., 2011; Modlmeier et al., 2014b; Pinter-Wollman, 2015; Pinter-Wollman et al., 2012; Segev et al., 2017; Traniello et al., 1984; Wray and Seeley, 2011). Additionally, weather (Pinter-Wollman et al., 2012), resource abundance (Bengston et al., 2014; Downs and Ratnieks, 2000; Pruitt and Goodnight, 2014), and environmental variation across their range can also greatly influence the collective behavior of groups (Bengston and Dornhaus, 2014; Bengston et al., 2014; Pankiw, 2003; Segev et al., 2017). But biotic factors, such as social environment, the presence or absence of predators, distance to neighbors, the presence of "keystone" individuals, adults, or queens, or previous group experience can also dictate group behavior (Keiser et al., 2018; Kleeberg et al., 2014; Laskowski and Pruitt, 2014b; Modlmeier et al., 2015b; Modlmeier et al., 2014e; Norman et al., 2017; Pamminger et al., 2011; Pruitt and Keiser, 2014a; Suryanarayanan et al., 2011; Suryanarayanan and Jeanne, 2008; Wright et al., 2016a; Wright et al., 2017b).

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

Now that we have outlined some mechanisms that can cause behavioral differences between societies, the next and perhaps more difficult endeavor is to discover how or why this variation is maintained. After all, if there are fitness costs and benefits associated with behaving a certain way, we might expect selection to act as a homogenizing force on within-colony behavioral variation and among-colony differences in collective personality. But the ubiquity of personalities within animal societies and across groups suggests both notions are false. We will now discuss some of the most salient causes of between-group behavioral diversity.

***Frequency-dependent selection***. The hawk/dove model is a classic model in game theory that describes how the costs and benefits associated with one behavioral strategy can be inversely related to an alternate strategy in a population (Smith, 1979). That is, the costs and benefits of a behavior are frequency-dependent, and can result in fluctuations in the genetic and behavioral makeup of a population (Nonacs and Kapheim, 2007, 2008). A similar phenomenon can occur in social groups, as opposed to a population, where different behavioral types enjoy a selective advantage relative to others, until a point is reached where the pendulum of selection begins to swing the other way. This type of selection keeps any one individual level BT from becoming fixed, and thus promotes behavioral diversity within a group over generations. We propose that similar forces could play a role in maintaining among-group variation in collective personality as well. Nearly every study examining the functional consequence of collective personality has detected directional selection on collective personality, but the maintenance mechanisms enabling this variation remains unscrutinized. We propose that frequency-and density-dependent selection acting on collective personality could be one such mechanism. The behavioral distribution of conspecifics may also drive group-level diversity, though this hypothesis remains untested. For instance, aggressive colonies may be favored in populations of strictly docile colonies, but suffer unreasonable costs that drive their performance beneath that of docile colonies when aggressive societies primarily interact with aggressive neighbors. The costs of aggressive-aggressive conflict at the colony level, a la the hawk-dove game, are plausibly quite high and could be fairly estimated.

***Social heterosis***. An individual's behavior can't be two things at the same time; they can't be simultaneously bold and shy, or aggressive and docile. But while individuals might be able to modulate their behavior somewhat throughout the day, the field of animal personalities rests on the observed fact that individuals are not infinitely plastic. Groups, however, face no such identity crisis. Unlike a single individual, a group can harbor as many genetic and behavioral variants as there are individuals, which allows for any mutual benefits of this diversity to be shared by all group members, and even the group as a whole. The benefit of within-group behavioral diversity is commonly referred to as “social heterosis”.

In the social spider *Anelosimus studiosis*, for instance, different colony compositions are selected in different habitats based on resource abundance (Pruitt and Goodnight, 2014). Furthermore, *A. studiosus* colonies of mixed (docile + aggressive) compositions outperform monotypic compositions in nature (Pruitt, 2013). Thus, environmental differences in resource availability and predator abundance/presence may be a large factor in maintaining colony-level behavioral variation in social taxa. Just like individuals, we reason that colony performance may be contingent on the phenotypic neighborhood in which it resides, and social heterosis at the level of the group is one plausible outcome. For example, one might propose that colonies surround by neighbors of unlike behavioral tendencies may compete less for resources, they may occupy different kinds nests, or they subtly partition their activities temporally in a manner that reduces conflict. We even propose that neighboring colonies may, over time, begin to behave more dissimilarly as to enjoy such benefits. More attention on such topics is sorely needed.

***Behavioral reaction norms***. Individuals often vary in their average behavior across contexts. But they also often vary in behavioral plasticity, or the degree to which they respond to changes in their environment. Previously, these two aspects of an individual—personality and plasticity—had been treated as separate entities. In fact, personality and plasticity had often been envisioned as two ends of a spectrum. If individuals are infinitely plastic, how can they be said to behave differently? However, these two factors are now seen as tightly intermingled. Simply put, a behavioral reaction norm approach describes how an animal varies in a certain behavior, say aggressiveness, over some environmental gradient, such as temperature, population density, or predation risk (Dingemanse et al., 2010). In a social group, one might expect selection on optimal response curves to erode group behavioral diversity and its genetic underpinnings, but limits and costs to plasticity at the individual level can allow such variation to persist. In some cases, such plasticity may even protect underlying genetic variation from the paring force of stabilizing selection (West-Eberhard, 2003). At the colony level, it is almost certainly true that entire societies will vary in their collective behavioral reaction norms. However, the functional consequences of the variability remain entirely unknown.

***Temporal tradeoffs***. Sometimes the behaviors that promote success in one life stage are suboptimal for a later life stage, and the same may be true across ecological contexts and situations as well. When this occurs, natural selection can pull in opposite directions depending on the time of year, the situation, or life stage of the organism, and this can help to maintain spatiotemporal variation in behavior (Wolf et al., 2007). We propose that conflicting selection pressures across situations could play an important role in the maintenance of genetic variation in collective personality as well (e.g., (Lichtenstein et al., 2015; Pruitt et al., 2017b)). Whether tradeoffs associated with collective behavioral types are common is mostly unknown, but the possibility is difficult to ignore. They merely wait to be examined, and the time is ripe (Table 1).

## Social Insect and Arachnid Societies

Some of our deepest understandings of collective personalities come from studies on social insects and spiders. We have already broadly covered some of the mechanisms that lead to and maintain behavioral variation and collective phenotypes. We will now review the current state of our knowledge surrounding collective personalities in the field's most prominent systems, and call attention to several perceived gaps in our knowledge. We will cover examples of how the personalities of group constituents shape the collective behavioral types of their groups, and how individual and collective personality interact with other elements of social ecology, including division of labor, colony defense, colony aggressiveness, collective decision making, and nest construction. It is an impossible task to truly discuss any one of these collective traits in isolation, as they are often interrelated both statistically and functionally. For instance, colony aggressiveness is often a major factor in colony defense, and exploration is both a component of foraging competence and a colony's interaction rate with rival groups. Thus, while we will attempt to discuss these traits in functional clusters, there is much unavoidable crossover.

## Social insects: what we do and do not know

***Division of labor***. Perhaps the most studied influence of individual personality on collective outcomes is personality-linked division of labor. Division of labor (DOL) describes a process where workers increase overall group productivity and efficiency by having different individuals specialize on different jobs. For social insects, this phenomenon has primarily been studied in the context of adaptive caste ratios or continuous morphological variation among workers (Holldobler and Wilson, 1990). Age-related DOL (or temporal polyethism), as exhibited in honeybees, has also been given its due attention (Seeley, 1982). Recently, however, DOL in association with individuals' personality types, rather than their morphology or age, has captured the attention of behavioral ecologists. This trend is notable because most social insect species lack discrete morphological castes beyond queens and workers. In the absence of distinct morphological differences, personality variation potentially provides another cryptic axis of functional diversity that can help to predict which workers will tend to perform which tasks, as well as their aptitudes for those tasks, and their propensity to engage in task switching. We argue that DOL can and should be considered a collective personality trait, since different groups can exhibit different degrees of DOL, and many models of DOL, such as response thresholds (Robinson, 1992) and personality-based models (Holbrook et al., 2014; Wright et al., 2014b), assume an innate, genetically-based mechanism for task participation. However, it is important to note that some models of DOL do not assume intrinsic differences among workers, and instead rely on interactions between workers and their physical or social environment. These include self-reinforcement (Theraulaz et al., 1998b), age demographic (Robinson et al., 1994; Seeley, 1982), social dominance (Vanhonk and Hogeweg, 1981), foraging for work (FEW) (Franks and Tofts, 1994), social inhibition (Huang and Robinson, 1992, 1996), and network models (Gordon, 1986, 1989) of DOL.

For many insect societies, the collective personalities are the result of individual variation in the fixed response thresholds of the group's constituents, which also shape which individual tend to perform which tasks inside of a society. In bees, for instance, variation in sucrose responsiveness between individuals dictates colony-level nectar foraging behavior (Pankiw and Page, 1999, 2003; Pankiw et al., 2001). Similar individual response thresholds, but for pheromones produced by larvae, influence recruitment to pollen (protein) foraging

(Pankiw et al., 1998). Individuals can vary in their response thresholds to a number of phenomena, such as task-related social interactions with larvae and other workers (Gordon, 1996), and individual differences in how workers respond to these interactions can produce marked differences collective behavior. In contrast to classical studies on individuals' fixed response thresholds, which are a sensory-based approach, studies on animal personality tend to focus on individuals' latency to participate in one task or the frequency with which they engage in it (Wright et al., 2014b). We propose that individuals' performance in personality assays might well be linked with their fixed response thresholds or perhaps even the flexibility of their thresholds in response to experience. If true, this would provide a plausible thread of cause and effect linking individual personality with explicit sensory biases, and help to mechanistically explain the large number of studies linking the personality composition of groups with colony level personality.

***Foraging, exploration, and boldness***. Differences in the collective foraging and exploratory tendencies of colonies have been the subject of much recent study, for several reasons. First, foraging is something social insects do mostly outside their nest, and it is therefore easy to observe in intact colonies in situ. Second, it is vital for colony growth and survival because it is how colonies discover and acquire resources (e.g., food, water, nesting materials) and new nesting locations. Boldness, on the other hand, is defined as the propensity of an individual to engage in risky behavior (Sloan Wilson et al., 1994). While *prima facie* it may seem that boldness bears no relation to foraging and exploration, these traits are often highly interdependent: foraging and exploration requires leaving the safety of the nest, and thus presents risk. In fact, boldness is often measured as the latency to enter a new environment, which is the necessary first step to exploration and foraging. It is therefore no surprise that studies on collective personality regularly detect associations between these aspects of colony activity.

Inter-colony differences in foraging behavior have been documented in ants and bees, though wasps, termites, and other social insects remain absent from the literature. Moreover, much of our current understanding of collective foraging comes from ants. In harvester ants, for instance, colonies often vary in their active foraging window: some colonies consistently begin foraging earlier each day, and cease foraging later than other colonies, which influences total resource intake and colony growth (Cole et al., 2008; Cole et al., 2010). This has been shown to be directly related to the colony's genetic diversity. Other work has shown that the proximate mechanism driving these inter-colony differences may be related to variation in how colonies regulate their foraging in response to environmental feedbacks (Gordon et al., 2011). However, colony survival is apparently not associated with overall foraging activity, at least in some species (Gordon, 2013b). Rather, in harvester ants, it is colonies that mitigate their foraging on hot and dry days that produce more daughter colonies (Gordon, 2013b), likely due to water conservation. Nearly identical results have been found in other ant species as well (Blight et al., 2016). In both instances, it appears that colony foraging behavior interacts with their risk-taking behavior in somewhat surprising ways.

In ants, relatively little has been done looking at the effects of exploration *per se* on colony performance. Usually, exploration is identified to be important as part of a syndrome with other group behaviors like aggressiveness or overall activity. Some studies, however, have linked inter-group foraging differences to differences in colony exploration and worker route learning ability (Pasquier and Gruter, 2016). In fire ants, differences in exploratory behavior are correlated with foraging, and predict colony growth in situ (Bockoven et al., 2015). In acorn ants, success in competition for nests between species was determined by an interaction between colony exploratory behavioral types. *Temnothorax longispinosus* performed best in rival house hunting when their opponent (*T. curvispinosus*) had similar exploratory tendencies to their own. Conversely, *T. curvispinosus* tended to win resource competitions for nests when their opponent (*T. longispinosus*) exhibited a contrasting exploratory behavioral type (Lichtenstein et al., 2015). Another house-hunting study, but in Argentine ants, observed colony-level differences in the speed and accuracy of collective house-hunting decisions (Hui and Pinter-wollman, 2014). Exploration, as well as other personality traits, is also thought to be a factor in biological invasions (Carere and Gherardi, 2013; Chapple et al., 2012), possibly due to its effects on resource competition. In Argentine ants, colonies from introduced ranges tend to be more explorative, and more aggressive, than colonies from their native ranges (Blight et al., 2017). Boldness, like exploration, also frequently forms a syndrome with other group personality traits like exploration and aggressiveness. But in at least one study, colony-level boldness was directly related to colony response to alarm pheromone, which could be important for colony defense (Chapman et al., 2011).

Studies on honeybees and bumblebees make up the remainder of collective personality studies on foraging studies in insects. Perhaps the most well-known example of honeybee collective behavior, and its consequences for fitness, is outlined in a study by Wray et al. (Wray et al., 2011). This study showed behavioral consistence in many colony-level traits, particularly foraging and defensive behavior. More defensive colonies also were better foragers, and this syndrome was positively correlated to both colony productivity and over winter survival. There have been many studies detailing the genetic basis for collective traits such as foraging and aggressiveness (Alaux et al., 2009; Breed et al., 2004; Guzman-Novoa et al., 2004; Hunt, 2007), but Wray and colleagues demonstrated that selection on these genes should be under strong selection, given that only 24% of new colonies survive their first winter in temperate climates (Seeley, 1978). In bumblebees, inter-colony differences in collective foraging have been shown to be influenced by innate color preferences and learning speed of workers (Raine and Chittka, 2007, 2008), and colony foraging remains consistent over a colony's lifespan (Evans and Raine, 2014). Lastly, anthropogenic factors, such as the use of agricultural pesticides, have been shown to negatively impact bumblebee foraging behavior, and potentially colony success (Gill et al., 2012), and exposure to such stressors provides one potential mechanism to explain non-adaptive differences in colony behavior.

***Defensive behavior and aggressiveness***. The ability of a colony to successfully defend itself, or defeat a rival, is vitally important for its survival. Therefore, small differences in this trait could have large implications during competition for resources (Bengston and Dornhaus, 2014; Cerda et al., 2013; Davidson, 1998; Parr, 2008; Rowles and O'Dowd, 2007). In some *Temnothorax* ants, for instance, more aggressive colonies exhibited greater defensive behavior against intruders (Modlmeier et al., 2014c), tend to be better foragers (Lichtenstein et al., 2016a) and prove more efficient at nest relocation (Modlmeier et al., 2014c). Highly aggressive *Aphaenogaster* ant colonies also tend to be better foragers, more thoroughly explore their environment, and are overall better conspecific competitors compared to more docile colonies (Blight et al., 2016). However, high aggressiveness appears to be a double-edged sword: more aggressive *Aphaenogaster* colonies continue to forage in dangerously high temperatures, resulting in increased mortality rates relative to less aggressive colonies (Blight et al., 2016).

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

Honeybees also display marked differences in collective aggressiveness (Breed et al., 2004; Breed and Rogers, 1991; Collins et al., 1982), and colony aggressiveness and defensive behavior is positively correlated with foraging behavior, which have been demonstrated to influence colony success. Colony-level defensive behavior is highly influenced by the behavioral distribution of its workers. Interestingly, one study showed that colonies composed of a 1:1 mixture of aggressive and docile bees displayed the most defensive behavior, but that colonies containing more individually aggressive bees are more hygienic than other compositions (Paleolog, 2009). This conveys that the links between the behavioral tendencies of individual group members and that of the collective are not always linear and intuitive. Honeybee colony aggressiveness is also shaped by a few particularly aggressive workers that recruit more docile bees to attack intruders, as indicated in co-fostered colonies of European (docile) and Africanized (aggressive) bees (Guzman-Novoa et al., 2004).

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

The trend among many of these systems is that aggressiveness is often an important component determining a group's ability to successfully defend itself, or win contests against competitors. Another pattern emerging from these studies is that increased aggressiveness, while predictive of success in a wide variety of contexts, can come with costs. Colony aggressiveness may therefore regularly be under balancing selection in many insect systems. Thus, we offer that researchers should use caution when reporting the benefits of colony aggressiveness when only a narrow set of contexts is considered. Furthermore, researchers performing manipulation studies (particularly those occurring in the lab) that appear to discover “optimal” collective phenotypes should be skeptical regarding the ecological validity of their results, especially if these “optimal” phenotypes deviate greatly from those observed in natural populations.

***Decision-making, cognition, and learning***. Between-individual variation in traits like cognition and learning might more appropriately be viewed as traits that may *inform* personality, rather than being a personality trait *per se* (Carere and Locurto, 2011; Griffin et al., 2015). Nevertheless, variation in traits such as cognition and learning are likely important in determining collective behaviors in insects such as choosing nesting sites (Mallon et al., 2001; Passino et al., 2008; Pratt et al., 2002; Seeley and Buhrman, 1999; Sumpter and Pratt, 2009), foraging (Beckers et al., 1993; Beekman et al., 2001), engaging in collective movements, or constructing complex three-dimensional structures. Overall cognitive capacity is larger in groups than individuals, suggesting that groups may be more adept at making optimal choices than individuals (Sasaki et al., 2013; Sasaki and Pratt, 2012), and that this accuracy may scale with group size. Different tasks performed within a colony might also have different cognitive demands, and thus, cognitive ability could determine how efficient individuals and, in turn, their colonies are at executing certain tasks (Reznikova, 2008). Some investigators have even argued that colonies themselves might profitably be viewed as single cognitive units (Sasaki and Pratt, 2018).

The bulk of studies investigating collective decision-making, cognition, and learning in social insects comes from work on ants and bee, often during nest choice. Colonies often must find alternative nest sites, which involves moving many different colony components (e.g., queens, broods, other workers). Nest sites also vary widely in quality, and colonies are known to prioritize some attributes over others (Visscher, 2007). In ants, while studies abound describing the processes involved in decision-making, from individuals up to their colonies, none to our knowledge have quantified between-colony variation in any cognitive trait. At least one study in *Temnothorax* ants, however, has demonstrated that nest relocation efficiency increases with increased colony aggressiveness (Modlmeier et al., 2014c), suggesting that collective personality represents another axis of decision-making strategies not captured by studies that evaluate group size effects. But, how aggressiveness may have influenced cognitive decision-making processes has not been investigated.

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

***Nest construction***. One of the most impressive collective behaviors of social insects is cooperative nest-building. These nest structures can vary widely in size and shape, from small inconspicuous piles of sand blocking nest entrances in *Temnothorax* ants, to large termite mounds from the genus *Macrotermes* that reach heights of 4 meters or more (2011). The building of many of these structures is a self-organizing process, where higher-level patterns emerge from the interactions between individuals eliciting both positive and negative feedback responses. These responses are mediated indirectly by stigmergy, a process where modifications of the environment by one individual stimulates the performance of a second modification by others (Bonabeau et al., 1997; Camazine, 1991; Karsai and Penzes, 1993; Theraulaz and Bonabeau, 1995; Theraulaz et al., 1998a; Theraulaz et al., 2002). However, despite the large variation of nest structures observed between species, and even within species, studies testing for consistent between-colony differences in nest architecture that control for environment are limited.

Between-colony variation in nest construction behavior has been observed in a handful of studies. *Temnothorax regatulus* ants can be found nesting in small rock crevices. Crevices vary in quality, but *T. regatutlus* prioritizes crevices with small openings, as these are often more easily defended (Visscher, 2007). When no ideal crevice presents itself, *T. regatulus* workers forage for small grains of sand and other debris, which they then use wall-in their crevice. In a study looking at the consistency of this wall-building behavior in *T. regatulus*, researchers found that individual colonies differed consistently in the wall architectures they constructed both across environment and repeated building events (DiRienzo and Dornhaus, 2017). The subterranean termite, *Reticulitermes speratus*, builds shelter tubes that protect individual termites while foraging. When groups of termites are separated from their colony, they still happily perform collective shelter tube-building. When researchers split larger colonies into smaller sub-colonies and observed their shelter tube-building, they found that sub-colonies from the same colony built similarly-patterned tubes that were distinct from the tubes build by sub-colonies created from foreign colonies (Mizumoto and Matsuura, 2013). These differences can be attributed to the degree of positive feedback exhibited, as well as the number of termites actively building the structures (Mizumoto et al., 2015). More studies are needed to understand the mechanisms driving nest variation across colonies, as well as their performance implications for societies.

One system ripe for evaluating the effects of nest architecture are tent caterpillars. These groups are known to perform a variety of collective behaviors (Casey et al., 1988; Costa and Ross, 2003; Fitzgerald and Costa, 1986; Fitzgerald and Peterson, 1988), and between-individual differences in activity, and its relation to individual growth rates, have already been established (Nerniroff and Despland, 2007). To what degree these individual differences scale to impact colony traits is yet unknown. Aphids behavior too is known to vary across genotypes; the situational parthenogenetic nature of these insects and their ease of manipulation likewise poises them for investigations on collective personality and colony performance in contrasting circumstances.

## Social arachnids: what we do and do not know

***Division of labor***. In arachnids, studies of personality-based DOL have been conducted in three genera: tangle web spiders in the genus *Anelosimus*, arid-dwelling spiders from the genus *Stegodyphus*, and the New Guinean social spider *Achaearanea wau* (Lubin, 1995). In *An. studiosus*, individuals within a colony exhibit one of two behavioral types, docile or aggressive (Pruitt et al., 2008), and this distinction predicts individuals' participation and proficiency at various tasks (Holbrook et al., 2014; Wright et al., 2014b). Docile individuals assume brood care duties, while aggressive spiders are more engaged in colony defense (Wright et al., 2014b). The degree of DOL in this species is high (Holbrook et al., 2014), on par with those of many social insects, such as bumblebees (Jandt and Dornhaus, 2009) and harvester ants (Holbrook et al., 2011; Jeanson and Fewell, 2008). In the field, colonies composed of only docile individuals grow more quickly but die off in fewer generations because of invasion by predatory inquilines. Conversely, aggressive colonies do not accumulate inquilines, but their deficient—and often cannibalistic—brood care practices prevent them from growing or proliferating as quickly as their docile rivals. Colonies with both docile and aggressive individuals enjoy highest overall success (Pruitt, 2012, 2013; Pruitt et al., 2012a; Pruitt and Riechert, 2011a, b). A closely related species, *Anelosimus exemius*, also exhibits DOL, but this is related to age (Settepani et al., 2013), body size, and body condition (Ebert, 1998) rather than personality. Three other social *Anelosimus* species—*A.*

*rupununi*, *A. guacamayos*, and *A. oritoyaku*—exhibited higher foraging success when colonies are composed of a mixture of docile and aggressive spiders, suggesting that these species may also exhibit some degree of DOL during foraging (Pruitt et al., 2012b). Recent work suggests that behavioral compositions could be locally adapted in on species of *Anelosimus*, and that this species may have evolved mechanisms of maintaining these optimal compositions if perturbed (Pruitt and Goodnight, 2014; Pruitt et al., 2017a). Little, however, is known about the proximate cues that individuals and/or groups use to execute these shifts or whether similar biology occurs in other social *Anelosimus*.

African desert social spiders from the genus *Stegodyphus* build a three-dimensional communal nest, and construct numerous two-dimensional capture webs that radiate away from it. Several *Stegodyphus* species exhibit between-individual variation in boldness which has been linked to colonies' DOL and collective behavioral type. For instance, participation in prey capture is positively related to individuals' boldness and negatively associated with body condition in *S. dumicola* (Keiser et al., 2014b; Wright et al., 2015; Wright et al., 2017b). *S. dumicola* has also exhibits DOL in defensive behavior, where bolder individuals are more likely to engage in defensive silk-spinning when attacked by predatory ants (Wright et al., 2016a). There is evidence that DOL increases over time as individuals become familiarized with nest mates, and conversely, sudden changes in group membership decreases group sucess in collective tasks and social niche construction (Laskowski et al., 2016b). In *S. sarisanorum*, boldness and condition were similarly related to participation in prey capture (Beleyur et al., 2015; Grinsted et al., 2013; Settepani et al., 2013). In *S. mimosarum*, DOL in prey capture has been linked to body size (Wickler and Seibt, 1993). Thus, across all three independently evolved social species of *Stegodyphus*, similar patterns of personality-based DOL emerge and appear to play a role in colony success.

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

***Foraging and boldness***. In arachnids, foraging behavior is by far the most well-studied aspect of collective personality. This is, in part, because the ability to subdue large prey has long been thought to underlie the evolution of sociality in these systems (Avilés and Guevara, 2017; Lubin and Bilde, 2007; Nentwig, 1985; Powers and Aviles, 2007; Pruitt and Avilés, 2017; Yip et al., 2008). Unlike in the above section on social insects, exploration will not be considered here because social arachnids often do not explore the environment beyond their nests and webs. Boldness, however, does appear to be linked to foraging efficiency in several social species. In *S. dumicola* and *S. sarisonorum* colonies, individuals vary in their boldness. In *S. dumicola*, between-colony variation in the proportion of bold individuals present is positively related to both the speed and magnitude of collective foraging response to simulated prey in both the lab and field (Grinsted and Bacon, 2014; Grinsted et al., 2013; Keiser et al., 2014b; Keiser and Pruitt, 2014; Lichtenstein et al., 2016b; Wright et al., 2015). Boldness in this species is also directly related to the propensity to transmit cuticular bacteria to other nest mates (Keiser et al., 2016b), and the proportion of bold individuals within a colony can influence the ease at which bacteria spread throughout a colony (Keiser et al., 2017), which could determine a colony's vulnerability to disease outbreaks. Participation is web repair is also positively associated with individuals' boldness in *S. dumicola* (Keiser et al., 2016c). Boldness further determines the degree to which an individual spider will exhibit a "keystone" behavioral phenotype. In behavioral ecology, keystone individuals are defined broadly as individuals that have a disproportionately large influence of group dynamics relative to their abundance in groups (Modlmeier et al., 2014d). In *S. dumicola*, bold individuals act as keystones because they catalyze greater task participation in shy colony members, which leads to a 400% increase in the number of attackers, and a -80% decrease in latency to attack prey (Pruitt et al., 2013; Pruitt and Keiser, 2014a). However, not all populations are susceptible to keystone influence. Putative keystones do not have any behavioral catalyzing effects on *S. dumicola* colonies from wet habitats, while colonies from arid habitats are highly susceptible to their influence (Pruitt et al., 2017b).

In social *Anelosimus*, collective foraging aggressiveness can be determined by the presence of aggressive or bold individuals. In *A. studiosus*, aggressive spiders are more likely to engage in prey capture, attacked prey more quickly, and secured prey more efficiently, than their docile nest mates (Holbrook et al., 2014; Pruitt et al., 2012a; Pruitt et al., 2008; Wright et al., 2014b), which makes colonies behave more aggressively in aggregate. Aggressive foraging behavior is linked with individual boldness in several other *Anelosimus* spiders, such as *A. domingo* and *A. eximius* (Pruitt et al., 2011).

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

In *S. dumicola*, colonies are frequently raided by predatory ants from the genus *Anoplolepis* (Henschel, 1998). *S. dumicola* colonies commonly experience high annual extinction rates of over 90% per year. In some years, nearly 80% of these colony extinctions are the result of ant attacks (Henschel, 1998). These attacks can wipe out an entire *S. dumicola* colonies in minutes (Wright et al., 2016a). During an attack by ants, *S. dumicola* spins walls of defensive silk to help impede ants from entering the spiders' nest, which leads to colony demise (Wright et al., 2016a). Participation in defensive silk-spinning behavior is positively associated with individual boldness, yet colonies containing a mixture of bold and shy spiders exhibit over two-times as much defensive silk-spinning behavior as monotypic colonies (Wright et al., 2016a). Here again, none additive effects of group composition on collective personality appear to be the norm rather than the exception. Finally, many of the links between individual and collective personality sense in *Stegodyphus* disappear when colonies are consistently subjected to predation risk, suggesting that some environmental conditions can remove the signature of collective personality by forcing all colonies into a singular behavioral tendency (Wright et al., 2017b).

***Decision making, cognition, and learning***. Many have viewed arachnid behavior as being primarily governed by instinct (Jackson and Cross, 2011; Jakob et al., 2011). However, numerous investigations on solitary spiders suggest this is not always the case (Herberstein et al., 2013; Peckmezian and Taylor, 2015; Wilcox and Jackson, 1998). To what degree social living promotes greater or reduced cognitive ability, often referred to as the *social brain* and *distributed intelligence hypotheses*, in social spiders and other arachnids is unknown. Studies on *S. dumicola* have shown that both individuals and whole colonies of spiders are capable of associative learning tasks using seismic cues (Holbrook et al., 2014; Pruitt et al., 2016). Evidence further suggests that information can be spread from trained to untrained spiders at different rates depending on the behavioral type of trained individuals (Pruitt et al., 2016). This is the only study investigating links between learning, personality, and collective behavior in arachnids to date. Thus, many avenues remain open to further exploration.

***Nest construction***. No current studies exist addressing collective personalities and the types/shapes/sizes of webs they construct, though this is an area worthy of investigation. We know from a study in *A. studiosus* that webs constructed by aggressive individuals retain prey 64% longer than webs constructed by docile spiders (Wright et al., 2014b). However, finer details of web structure between the two behavioral types was not investigated. In *S. dumicola*, the shape of the substrate architecture available to construct capture webs influences both the mean and repeatability of collective foraging behavior across colonies (Modlmeier et al., 2014b), conveying that architectural differences in the landscape surrounding colonies is likely to constrain the kinds of collective behavior they exhibit. Future studies that more finely quantify aspects of web architecture in association with colonies' collective behavioral type or the distribution of behavioral types of their workers are still needed.

## Similarities and differences

Social insects and arachnids differ in many ways that may influence how groups behave collectively, and which collective personality traits may be favored by natural selection. Some of these differences include the ways insects and arachnids found colonies, colony mobility, foraging strategies, degree of interactions with local competitors, group mortality rates, intra-colony relatedness, as well as sensory modalities. We will now briefly discuss how differences in life history traits between social insects and arachnids may guide differences in the group-level traits we have discussed in the previous sections.

***Division of labor***. One commonly observed phenomenon in social insects and arachnids is that within-colony DOL tends to increase with group size (Gautrais et al., 2002; Holbrook et al., 2011; Robinson, 1992). This is because, as colonies grow, they become more complex and it pays to be more fastidious in work organization. While colony sizes in arachnids varies from two to several thousand individuals, colony sizes approach 100,000 in honeybees and more than 1,000,000 in some wasps, ants, and termites (Bourke, 1999). Furthermore, social insects need to perform numerous complex tasks that are wholly absent in arachnid societies, including active foraging for resources such as food, water, and nesting materials. This requires insect societies to be comparatively active, and DOL may help to avoid resource bottlenecks. In contrast, arachnid societies passively wait for prey to become ensnared, and spiders produce their own nesting materials endogenously. Both societies engage in brood care and the feeding of young. Finally, the lack of morphological castes in arachnid societies further conveys they may be limited in the levels of task specialization they can achieve. Despite these observations, the small number of studies on DOL in social arachnids have revealed surprisingly high levels of DOL, especially for the small experimental group sizes investigated (Holbrook et al., 2014; Wright et al., 2014b). Thus, relative to their size, arachnid societies appear to have higher levels of task specialization and associated task efficiencies than their social insect counterparts. One might argue that their collective personalities are therefore comparatively more *orderly* — the one exception being the obligate sterility and reproductive division of labor that characterize the eusocial insects. More studies on DOL and the mechanisms governing task specialization in both groups are needed to reveal any true consistent differences in how they organize work, and whether differences in DOL are functionally significant in situ.

***Foraging, exploration, and boldness***. Insect and arachnid societies differ in the ways they explore and acquire resources and interact with their environment. For example, insect societies are often initiated by one or sometimes a few individuals. These queens, or foundresses, search their environment for suitable nesting sites according to various criteria. Once a nesting site is chosen, these individuals must then explore their environment for building materials, and must continually forage for food and water to produce eggs and feed young. When workers emerge, they then take over these foraging and defensive tasks. Foraging in social insects is quite often individualistic, where single foragers explore their surroundings for resources. Once a resource is discovered, they can recruit others to help if needed. In social spiders, gravid females occasionally disperse long distances via “ballooning” (Schneider et al., 2001). This process involves producing a silken parachute of sorts, and having the wind take them where it may. This method of dispersal is completely passive, and involved no exploration. Likewise, social spiders do not forage similarly to social insect colonies. Rather than individually exploring their environment for resources, social spiders sit and wait for prey to become ensnared, and quickly attack as a group when this occurs. Thus, prey capture in social spiders is orchestrated and quickly executed, baring closer resemblance to prey capture in a pride of lions than to any social insect. For these reasons, studies on collective exploratory tendencies and activity level assays are almost wholly absent in social spiders, and research instead focuses on more salient traits such as boldness and foraging aggressiveness toward prey. Other social arachnids, however, such as the social huntsman *Delena cancerides*, which actively hunt their prey, might be more amenable to studies focusing on collective foraging and exploration. This species hunts prey solitarily, like some species of wasps and ants, but then shares some portion of this prey with fellow colony mates (Yip and Rayor, 2011, 2013).

Collective exploration and boldness, however, may be more relevant in social spiders during the process of founding colonies via “bridging.” Bridging occurs when individuals send out strands of silk that anchor to a nearby bush (Schneider et al., 2001). Spiders then chain along these silken bridges and found a new colony together. It would be interesting to observe whether individual or colony-level boldness positively correlates with bridging behavior versus ballooning, and how this changes colony life history patterns in association with their collective behavioral tendencies. Once a new bush has been colonized, it is conceivable that pioneering individuals explore the new habitat for the best suitable site. Habitat selection in many social arachnids is unknown, save for species that occupy limited real estate in rock cavities and under the bark of trees such as *D. cancerides* (Rowell and Aviles, 1995).

Currently, given the vast differences in life history between social insects and arachnids, it is no surprise that social insects currently outpace social arachnids in studies pertaining to collective foraging, exploration, and boldness. However, social spiders currently appear to be outpacing social insects in studies using an animal personality framework, likely owing to the ease at which spider societies can be manipulated in the lab, and career biases. Social spider colonies also remain where they are deployed, due to their limited dispersal capabilities, and this enhances their tractability for experimental studies in situ. However, we note that there are several insects, including familiar models (paper wasps, honeybees) and lesser-known models (aphids, tent caterpillars) in which experimental colonies can be generated and deployed. Thus, careful selection of one's focal system and questions is likely key.

***Defensive behavior and aggressiveness***. The ecological and life history differences between social insects and arachnids, particularly regarding their nesting structures and individual morphology, influences how these societies respond to predators, competitors, and general disturbances to their colonies. Many social insects, such as ants, bees, and wasps can respond to a larger range of threats, from small arthropods to much larger vertebrates, than arachnids. This is perhaps owing to insects' ability to leave their nests, *en masse*, with several thousand venomous, stinging, biting, and often flying, individuals. Most vertebrates, in contrast, have little to fear from social arachnids, as these societies are often smaller, and individuals are incapable of flying and stinging, and their bites are often ineffective. Only a handful of studies have investigated defensive behavior in social arachnids (Keiser et al., 2015a; Pruitt, 2013; Wright et al., 2016a; Yip, 2014), while colony defensive behavior has been documented across a broad swath of social insect taxa (Breed et al., 2004; Eisner et al., 1976; Judd, 1998). We therefore might predict strong positive selection on collective defensive behavior in social insects as compared to arachnids.

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

One notable similarity between social spiders and ants appears to be tradeoffs associated with aggressiveness. In ants, more aggressive societies tend to have increased foraging activity. While this appears to enhance resource acquisition, this also results in higher worker mortality due to overactive foraging in unfavorable environmental conditions. Colonies that take a more nuanced approach to foraging, and mitigate foraging in adverse conditions tend to be more successful. Similarly, in *A. studiosus* spider colonies, laboratory studies showed that colonies composed of more aggressive spiders performed better across the board. It had even been postulated that docile spiders were do-nothing social parasites. However, field studies demonstrated that aggressiveness came with great costs—colonies composed of more aggressive spiders cannibalized their own young, and did not provision young proficiently. In situ, mixed colonies enjoyed greater overall fitness. In the African social spider *S. dumicola*, a similar phenomenon occurs. In the laboratory and field, numerous studies demonstrated that more aggressive colonies (which are composed of bolder individuals) attacked prey faster, and attacked with more individuals than docile colonies (Keiser and Pruitt, 2014; Wright et al., 2015). However, colonies of mixed composition exhibit twice as much defensive behavior when being raided by predatory ants (Wright et al., 2016a), which may help explain why mixed colonies are the norm in the wild. We believe this tradeoff may be common across many social taxa, invertebrate or otherwise.

***Decision making, cognition, and learning***. There are many reasons to suppose that selection on traits like collective cognition, learning, and collective decision-making should differ between social insects and arachnids. Social insects interact with their broader environments much more intimately than most arachnid societies in almost all aspects. Thus, we might expect a higher capacity for collective learning and information transfer in social insects relative to arachnids, especially in a spatial and visual learning and memory. We see evidence for this in bumblebees, where there is a link between colony and individual learning speed and visual memory (Raine and Chittka, 2012). This individual variation in learning scales up to the collective behavioral tendencies of colonies, where learning speed is directly related to the amount of nectar a colony acquires (Raine and Chittka, 2007). Honeybees also have high demands for visual learning and memory (Zhang et al., 1999). When a new resource patch is discovered, individual workers must gather information about the quality, distance, and direction of floral resources and communicate this information back to naïve workers in a dance (Detrain and Deneubourg, 2008). This also occurs when honeybee colonies need to relocate to a new nesting site (List et al., 2009; Seeley, 1985; Seeley and Visscher, 2004). And, many ant species also rely on spatial learning and memory in house-hunting and collective foraging (Detrain and Deneubourg, 2008; Mallon et al., 2001; Pratt et al., 2002; Sumpter and Pratt, 2009).

Arachnid societies, on the other hand, might perform as well or better than insects on associative learning and memory tasks, especially via seismic cues, given that predator/prey vibratory discrimination tasks characterize most of their actions. As mentioned above, this type of collective learning and information transfer had been demonstrated in *S. dumicola* spiders (Pruitt et al., 2016). Social arachnids have poor eyesight, thus visual learning tasks are not relevant for this system. Studies on collective cognition in arachnids are also needed to determine how/whether group cognitive ability scales with group size as seen in some social insects. While there are an ever growing number of studies linking individual personality with learning styles, the intersection of collective personality and group cognition is a wide-open field with many discoveries waiting to be made.

***Future directions***. While the literature on collective personality has been steadily growing, this field is still in its infancy. For instance, although many studies have linked collective personality with colony performance, very few of these studies have been conducted in situ. Field studies are likely to be particularly illuminating because they may reveal situational costs and benefits to colonies' collective behavioral tendencies that would be difficult to forecast or characterize in lab studies. In essence, we argue that by approaching collective personality traits with the same framework that evolutionary behavioral ecologists approach individual traits, we are likely to enhance our understanding of how and why collective behavioral traits evolve, how they interact with colonies' life history and niche, and the degree to which such traits can respond to selection.

We believe there are many interesting and currently untouched areas in collective behavior awaiting thorough investigation. For instance, in groups that experience fission-fusion dynamics, how might collective personalities change as groups fractionate or merge? Does group personality influence collective cognition and inform group decision-making? Can parasites modify or exploit the collective behavior of a group to their own advantage similar to the way some entomopathogenic fungi manipulate the behavior of individuals (Andersen et al., 2012; Lefevre et al., 2009)? We therefore conclude with a brainstorming table of themes and hypotheses that relate collective personality to a large variety of other fields in evolutionary behavioral ecology (Table 2) that move beyond merely echoing the classic and foundational inferences in Table 1. However, the types of studies found in Table 1 will obviously often serve as the preconditions necessary for testing the questions and hypotheses in Table 2. These hypotheses are meant to inspire interested parties, and especially new graduate students, to think diversely about how the collective behavioral tendencies of whole groups stand to influence group functioning and success, as well as how groups interact in a broader ecological context in populations and communities. These are just a few areas in which we believe large discoveries could be made should they be given adequate attention.

## Conclusions

The aim of this review has been to broadly survey our current knowledge surrounding collective animal personalities, and the progress that has been made since the 2013 review on collective personalities by Jandt and colleagues (Jandt, 2013). In ants, we have seen some progress in moving out of the laboratory and into the field, which has produced valuable information about tradeoffs between foraging activity and colony success in variable environments (Gordon, 2013b; Gordon et al., 2013; Gordon et al., 2011). Honeybees, too, have enjoyed success in testing colony personality in the field, and relating it to colony fitness (Wray et al., 2011), though more studies on the benefits of colony personality in various environments could potentially illuminate mechanisms driving inter-colony differences in behavior. Bumblebees, alternatively, have served as prominent model systems for colony learning and speed-accuracy tradeoffs (Evans and Raine, 2014; Ings et al., 2009; Raine and Chittka, 2008, 2012), though field studies relating personality directly to fitness are rare (Raine and Chittka, 2005; Raine and Chittka, 2008). Personality work in social wasps and termites is currently in its infancy (but see (Mizumoto et al., 2015; Mizumoto and Matsuura, 2013; Wright et al., 2017a; Wright et al., 2016b)), and we greatly urge researchers to turn their gaze to these diverse, yet understudied, groups. Social arachnids, on the other hand, though a much less diverse group when compared to social insects, compose more than their market share of laboratory and field studies on collective behavior. However, work on collective learning and cognition is well behind that of social insects, and we believe there are many impactful discoveries to be made in arachnid cognition and learning.

Collective personality, as a framework, has the potential to broadly inform our understanding of social evolution and the evolution of collective phenotypes and their pros and cons in contrasting environments and situations. If we have succeeded, this review will have served as both a roadmap and compass for pushing the field of collective personalities forward.

## Table headers:

**Table 1**: This table summarizes some of the classic foundational hypotheses relating to collective behavior, and details the specific traits, time scales, and taxa that have been investigated over the last 8 years. These hypotheses often serve as a foundational starting point when new systems are being studied. For systems that have this groundwork established, we recommend researchers focus on testing the hypotheses in Table 2. For new or understudied systems (e.g. wasps and termites), we suggest researchers begin their point of inquiry relating to one or all the hypotheses outlined below.

**Table 2**: General questions and specific hypotheses relating to collective personality that remain open to investigation. In systems where foundational questions pertaining to collective personality (Table 1) have been achieved, we suggest researchers pursue the frontier questions outlined below.

**Table 1**:

| Hypothesis | Collective Personality Trait | Temporal Scale | Taxa | Source |
|---|---|---|---|---|
| ***H1: Groups exhibit stable differences in collective behavior*** | Collective Aggressiveness | Days | Ants | Lichtenstein et al. (2015), Marting et al. (2017), Weirnasz et al. (2014) |
| | | | Spiders | Pruitt et al. (2013), Pruitt & Keiser (2014) |
| | | Weeks | Ants | Bengston & Dornhaus (2014), Blight et al. (2017), Scharf et al. (2012) |
| | | | Bees & Wasps | Wray et al. (2011) |
| | | Months | Ants | Blight et al. (2015,2016), Buczkoski & Silverman (2006), Crosland (1990) |
| | | | Bees & Wasps | Pearce et al. (2001) |
| | | One year | Ants | Suarez at al. (2002) |
| | Exploratory and foraging behavior | Days | Ants | Marting et al. (2017), Gordon et al. (2011), Lichtenstein et al. (2015) |
| | | | Bees & Wasps | Raine & Chittka (2008) |
| | | | Fish | Jolles et al. (2018) |
| | | Weeks | Ants | Bengston & Dornhaus (2014), Blight et al. (2017), Bockoven et al. (2015), Scharf et al. (2012) |
| | | | Bees & Wasps | Wray et al. (2011) |
| | | Months | Ants | Blight et al. (2015, 2016) |
| | | Years | Ants | Cole et al. (2010), Gordon et al. (2013) |
| | Nest repair/relocation | Days | Ants | Cronin et al. (2015) |
| | | | Cockroaches | Planas-Sitja et al. (2015) |
| | | Weeks | Ants | Scharf et al. (2012) |
| | | | Bees & Wasps | Wray et al. (2011) |

| Hypothesis | Collective Personality Trait | Member Trait | Taxa | Source |
|---|---|---|---|---|
| ***H2: The personality scores of group members determine the collective personality of the group*** | Aggressiveness | Aggressiveness | Ants | Modlmeier et al. (2014) |
| | | | Bees & Wasps | Rittschof et al. (2017) |
| | | Boldness | Bees & Wasps | Wright et al. (2017) |

| | | | | |
|---|---|---|---|---|
| | | | Spiders | Pruitt et al. (2013), Pruitt & Keiser (2014), Pruitt & Pinter-Wollman (2015), Wright et al. (2015) |
| | Exploratory and foraging behavior | Activity level and sociability | Fish | Brown & Irving (2013), Jolles et al. (2017) |
| | | | Lepidopterans | Dussutour et al. (2008) |
| | | Boldness | Fish | McDonald et al. (2016) |
| | | Exploratory behavior | Birds | Aplin et al. (2014) |
| | | | Slime molds | Vogel et al. (2015) |
| | Nest repair/relocation | Activity level | Termites | Mizumoto et al. (2015) |
| | | Aggressiveness | Ants | Modlmeier et al. (2014) |
| | | Exploratory behavior | Ants | Hui & Pinter-Wollman (2014) |

| **Hypothesis** | **Collective Personality Trait** | **Performance Metric** | **Taxa** | **Source** |
|---|---|---|---|---|
| ***H3: Collective personality predicts colony performance*** | Aggressiveness | Contests over resources | Ants | Bengston & Dornhaus (2015), Blight et al. (2015), Lichtenstein et al. (2015) |
| | | Colony mass | Bees & Wasps | Wray et al. (2011) |
| | | | Spiders | Pruitt et al. (2017), Pruitt & Keiser (2014) |
| | | Damage to nest | Ants | Weirnasz et al. (2014) |
| | | Host plant health | Ants | Marting et al. (2017) |
| | | Repelling parasites | Ants | Jongepier et al. (2014), Pamminger et al. (2011, 2012) |
| | | Survival and reproduction | Spiders | Pruitt et al. (2017) |
| | Exploratory and foraging behavior | Contests over resources | Ants | Bengston & Dornhaus (2015), Blight et al. (2015), Lichtenstein et al. (2015) |
| | | Colony mass | Bees & Wasps | Wray et al. (2011) |

| **Hypothesis** | **Collective Personality Trait** | **Life History Trait** | **Taxa** | **Source** |
|---|---|---|---|---|
| ***H4: Collective personality shapes colony life history*** | Aggressiveness | Productivity | Ants | Bengston et al. 2016, Blight et al. (2016), Bockoven et al. (2015), Scarf et al. (2012) |
| | | Reproductive investment | Ants | Bengston et al. (2016) |
| | Exploratory and foraging behavior | Productivity | Ants | Bengston et al. (2016), Blight et al. (2016) |
| | | Reproductive investment | Ants | Bengston et al. (2016) |

| | | | |
|---|---|---|---|
| Nest repair/relocation | Productivity | Ants | Scharf et al. (2012) |

**Table 2**:

| General question | Specific Hypotheses |
|---|---|
| **Q1: In colonies that experience fission-fusion dynamics, how do the personalities of groups change as they divide or merge?** | |
| | ***Hypothesis 1a***: In social species whose colonies fragment, daughter colonies will initially resemble their mother colony in collective personality. |
| | ***Hypothesis 1b***: Daughter colonies will develop distinct collective personalities, which predict division of labor within the super-colony. |
| | ***Hypothesis 1c***: Variation in collective personality between the nests of a single polydomous colony can change to benefit the super-colony, akin to division of labor across multiple nests. |
| **Q2: Do colonies' collective behaviors determine non-linear relationships between colony mass and metabolism?** | |
| | ***Hypothesis 2a***: The presence of seemingly inactive "lazy individuals" will reduce colony metabolic rate and collective activity level. |
| | ***Hypothesis 2b***: The metabolic rate of active colonies will scale like single organisms, whereas the metabolic rates of inactive colonies will plateau at a shallower threshold. |
| | ***Hypothesis 2c***: The presence of inactive individuals will be locally adapted (perhaps in patchy resource areas), driving geographic variation in metabolic scaling patterns driven by collective personality. |
| **Q3: Colony Personality and Collective Cognition/Learning** | |
| | ***Hypothesis 3a***: Groups will differ in their collective cognitive capacity based on the cognitive capacities of individual constituents. |
| | ***Hypothesis 3b***: Groups will differ in collective learning based on the distribution of learning types within the group (e.g., proportion or presence of associative vs. spatial learners). |
| | ***Hypothesis 3c***: Groups will perform better at certain tasks based on the learning types they contain. For instance, spatial learners might be better foragers, whereas associative learners might defend their colonies more closely. |
| | ***Hypothesis 3d***: Mixed colonies will benefit from having a diversity of learning types, based on environmental/population differences such as food abundance or threat level. |
| | ***Hypothesis 3e***: The presence of one or a few individuals of high cognitive ability will be sufficient to drive fast collective learning rates and low error rates for the group. |
| **Q4: Do groups exhibit consistent differences in their decision-making strategies?** | |
| | ***Hypothesis 4a***: Different colonies will consistently tend to favor *speed* over *accuracy* and vice versa during migrations to new nests. |

***Hypothesis 4b***: Different colonies will consistently tend to favor *cohesion* over *speed* and vice versa during migrations to new nests.

***Hypothesis 4c***: Low nest competition will favor high accuracy, which will require more time, and high competition favors high speed.

**Q5: Can autocorrelation of group-level personality be used as an indicator of incipient group collapse?**

***Hypothesis 5a***: Groups will exhibit stable colony personalities across their lifespans with some stochastic variation and predictable seasonal variation.

***Hypothesis 5b***: The emergence of reduced temporal autocorrelation or increased within-colony variance in personality will signal the collapse or disbanding of a group.

***Hypothesis 5c***: The emergence of reduced temporal autocorrelation or increased within-colony variance in personality will precede other indicators of colony collapse such as increase internal violence, decreased nest maintenance, and decreased reproductive rate.

***Hypothesis 5d***: Across the lifespans of colonies, predictable patterns in collective personality will emerge.

**Q6: Do collective personalities of colonies determine their interior carrying capacity and population biology?**

***Hypothesis 6a***: Colonies will have internal carrying capacities and intrinsic growth rates specific to colonies that depend on their collective personalities.

***Hypothesis 6b***: The collective personality of colonies will determine their intra-colony intrinsic growth rate and carrying capacity.

***Hypothesis 6c***: Colonies with low intra-colony carrying capacities and intrinsic growth rates will grow and reproduce less readily.

***Hypothesis 6d***: Populations composed of colonies with low carrying capacities and intrinsic growth rates will be more stable, will reach higher densities of colonies, and be less likely to overshoot their population carrying capacity.

**Q7: Can parasites shape colony personality to increase parasite reproduction and dispersal?**

***Hypothesis 7a***: Social parasites will manipulate the collective behavior of groups to further their own propagation (increase affinity to foreign conspecifics, decrease colony aggressiveness so more parasites can infect colony, increase exploration so parasites can propagate easier, etc.).

***Hypothesis 7b***: Infected colonies will differ behaviorally from uninfected colonies, and this difference in collective behavior increases the infection risk of neighboring colonies and increases host colony competence.

**Q8: Do colonies' collective personalities influence associated inquiline communities?**

***Hypothesis 8a***: Non-aggressive colonies will foster more inquilines and associated animal life, thereby destabilizing the colonies.

***Hypothesis 8b***: Aggressive colonies will repel inquilines, and consequently will not benefit from potential mutualistic interactions with inquilines.

***Hypothesis 8c***: Colonies with moderate aggressiveness and greater intracolonial behavioral diversity will foster an intermediate load of inquilines that involve more mutualistic interactions.

***Hypothesis 8d***: Colonies of intermediate aggressiveness and mutualistic interactions with inquilines will be more temporally stable than extremely aggressive and docile colonies.

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**Q9: To what degree does the evolution of colony personality mimic the evolution of individual level traits?**

***Hypothesis 9a***: The heritability of colony personality is greater in colonies that operate more as a single selective unit (e.g., highly eusocial societies, inbred groups) or in instance where societies are established by a single or group of related foundresses.

***Hypothesis 9b***: Among-group variation in collective personality and the effectiveness of selection on it positively co-varies with the level of genetic divergence across groups

***Hypothesis 9c***: Negative frequency-dependent selection and cross-contextual trade-offs associated with colony personality acts to maintain heritable variation in colony traits within populations.

***Hypothesis 9d***: Colonies surrounded by neighbors of unlike collective personality will compete less for resources, and increase the collective performance of that neighborhood of colonies.

***Hypothesis 9e***: Through time, neighboring colonies will exhibit stronger differences in their collective personalities to adopt distinct niches and reduce competition across societies.

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**Q10: Colony Personality & Queen Number and Behavior: Are polygynous colonies (multiple queens) aggressive than monogynous colonies (single queen) towards intruders?**

***Hypothesis 10a***: Workers from polygynous colonies will be less aggressive to foreign queens and other intruders.

***Hypothesis 10b***: Polygynous colonies will be more willing to accept and rear foreign queens than monogynous colonies, due to reduced overall collective aggressiveness.

***Hypothesis 10c***: Polygynous colonies will be more susceptible to parasitism by inquilines.

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**Q11: How does collective personality determine tolerance/affinity of neighbors?**

***Hypothesis 11a***: Presence of highly aggressive colonies members will increase collective aggressiveness of colonies, and yet aggressive individuals will be more likely to perish in fights between colonies.

***Hypothesis 11b***: On a short time scale, aggressive interactions between colonies will decrease collective aggressiveness by depleting aggressive individuals.

***Hypothesis 11c***: Colonies that quickly create aggressive individuals and recover their collective aggressiveness will outcompete colonies still depleted of aggressive individuals.

***Hypothesis 11d***: Cycles of colonies depleting and replenishing aggressive individuals will lead to arms race to create more and more aggressive colonies.

***Hypothesis 11e***: Colonies with very low aggressiveness may outperform aggressive colonies when aggressive colonies are at high representation, because they avoid the cost of inter-group conflict, akin to a colony level hawk-dove game.

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**Q12: How does collective personality relate to the social responsiveness or social susceptibility of its members?**

***Hypothesis 12a***: The social responsiveness of a colony will depend on the behavioral distribution of its individuals. Certain behavioral types (e.g. docile or shy types) will be more responsive to fellow group members than others.

***Hypothesis 12b***: The behavioral types that are socially responsive to the behavior of fellow colony members (e.g., shy individuals) may not be the most socially responsive to individuals from other colonies (e.g., aggressive individuals).

***Hypothesis 12c***: Colonies' social responsiveness will have a concave-down relationship with state (starvation level, condition, infection status): small reductions in colony condition will increase social responsiveness before reaching such threshold where responsiveness to fellow colony members and enemies alike will drop off dramatically.

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**Q13: How does collect personality influence horizontal transmission of group members across colonies?**

***Hypothesis 14a***: Less collectively aggressive colonies will be more likely to exchange individuals, whereas aggressive colonies will be more likely to retain members and repel interlopers.

***Hypothesis 14b***: The transmission of individuals between colonies will erode between-colony behavioral variation.

***Hypothesis 14c***: Polydomous (multi-nest) colonies will exchange more individuals than monodomous colonies, thereby homogenizing inter-subcolony behavioral variation.

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**Q14: Can colony mortality and collective behaviors form positive feedback loops?**

***Hypothesis 15a***: Colonies that exhibit a reduced tendency to forage, defend themselves, or engage in hygienic behaviors will suffer increased mortality of colony members.

***Hypothesis 15b***: The mortality of colony members will reduce collective foraging, defense, and hygienic behaviors at the colony level, and may bias the representation of personality types in the remaining members.

***Hypothesis 15c***: Mortality of group members and reduced collective foraging, defense, and hygienic behavior will form positive feedback cycles that leads to colony collapse.

***Hypothesis 15d***: The beginning of this feedback cycle will generate reduced temporal autocorrelation and increases in within-colony variance in collective personality, foretelling of imminent collapse.

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**Q15: Does social heterosis (i.e., within-colony behavioral diversity) generate variation in the flexibility of collective behavior?**

***Hypothesis 16a***: Diversity in member colony personality will beget greater behavioral flexibility in collective behavioral tendencies.

***Hypothesis 16b***: Colonies with more flexible collective personalities will prove more successful at exploiting a range of resources and conditions, whereas more consistent colonies will before better than flexible colonies only under a narrow range of environmental conditions.

***Hypothesis 17d***: Stable environments will select for behavioral consistency in collective personality, whereas dynamic environments will favor greater plasticity in collective personality.

**Q16: How does collective personality shape patterns of niche construction by large colonies?**

***Hypothesis 17a***: The collective personality of large social arthropod colonies will change how they alter local ecosystem or community properties (e.g. deposits of nutrients, excessive nest structures, or inquiline communities).

***Hypothesis 17b***: Such alterations to local environments will favor the performance of certain collective behavioral phenotypes, often of the phenotypes of the colonies that made them.

***Hypothesis 17c***: When a collective behavioral phenotype alters the local environment, and the local environment in turn favors that collective behavioral phenotype, can generate a feedback loop.

***Hypothesis 17d***: Behavior vs. local environment feedback loops could generate behavioral correlations. For instance, intense collective foraging may create large midden heaps, which might attract parasites or predators, and this might favor collective aggressiveness. This result would be a correlation between collective foraging and collective aggressiveness.

# Literature Cited

Agnarsson I, 2006. A revision of the New World eximius lineage of Anelosimus (Araneae, Theridiidae) and a phylogenetic analysis using worldwide exemplars. Zoological Journal of the Linnean Society 146:453-593.

Agnarsson I, Avilés L, Coddington JA, Maddison WP, 2006. Sociality in Theridiid Spiders: Repeated Origins of an Evolutionary Dead End. Evolution 60:2342.

Alaux C, Sinha S, Hasadsri L, Hunt GJ, Guzman-Novoa E, DeGrandi-Hoffman G, Uribe-Rubio JL, Southey BR, Rodriguez-Zas S, Robinson GE, 2009. Honey bee aggression supports a link between gene regulation and behavioral evolution. Proceedings of the National Academy of Sciences of the United States of America 106:15400-15405.

Ament S, Corona M, Pollock H, Robinson G, 2008. Insulin signaling is involved in the regulation of worker division of labor in honey bee colonies. Proceedings of the National Academy of Sciences. p. 4226-4231.

Ament SA, Wang Y, Robinson GE, 2010. Nutritional regulation of division of labor in honey bees: toward a systems biology perspective. Wiley Interdisciplinary Reviews-Systems Biology and Medicine 2:566-576.

Amir N, Whitehouse MEA, Lubin Y, 2000. Food consumption rates and competition in a communally feeding social spider, Stegodyphus dumicola (Eresidae). Journal of Arachnology 28:195-200.

Andersen SB, Ferrari M, Evans HC, Elliot SL, Boomsma JJ, Hughes DP, 2012. Disease Dynamics in a Specialized Parasite of Ant Societies. Plos One 7.

Aparicio JM, Bonal R, Munoz A, 2007. Experimental test on public information use in the colonial Lesser Kestrel. Evolutionary Ecology 21:783-800.

Aplin LM, Farine DR, Mann RP, Sheldon BC, 2014. Individual-level personality influences social foraging and collective behaviour in wild birds. Proc R Soc B-Biol Sci 281.

Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC, 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature 518:538-541.

Aviles L, Purcell J, 2012. The Evolution of Inbred Social Systems in Spiders and Other Organisms: From Short-Term Gains to Long-Term Evolutionary Dead Ends? Advances in the Study of Behavior, Vol 44 44:99-133.

Avilés L, Guevara J, 2017. Sociality in Spiders. Cambridge (UK): Cambridge University Press.

Barry MJ, 1994. The costs of crest induction for Daphnia carinata. Oecologia 97:278-288. doi: 10.1007/bf00323161.

Barth RH, Lester LJ, Sroka P, Kessler T, Hearn R, 1975. Juvenile-hormone promotes dominance behavior and ovarian development in social wasps (Polistes-annularis). Experientia 31:691-692.

Beckers R, Deneubourg JL, Goss S, 1993. Modulation of trail laying in the ant lasius-niger (hymenoptera, formicidae) and its role in the collective selection of a food source. Journal of Insect Behavior 6:751-759.

Beekman M, Sumpter DJT, Ratnieks FLW, 2001. Phase transition between disordered and ordered foraging in Pharaoh's ants. Proceedings of the National Academy of Sciences of the United States of America 98:9703-9706.

Beleyur T, Bellur DU, Somanathan H, 2015. Long-term behavioural consistency in prey capture but not in web maintenance in a social spider. Behav Ecol Sociobiol 69:1019-1028.

Bell AM, Sih A, 2007. Exposure to predation generates personality in threespined sticklebacks (Gasterosteus aculeatus). Ecology Letters 10:828-834.

Ben-Shahar Y, Robichon A, Sokolowski MB, Robinson GE, 2002. Influence of gene action across different time scales on behavior. Science 296:741-744.

Bengston S, Jandt JM, 2014a. The development of collective personality: the ontogenetic drivers of behavioral variation across groups. Frontiers in Ecology and Evolution 2:81.

Bengston SE, Dornhaus A, 2014. Be meek or be bold? A colony-level behavioural syndrome in ants. Proceedings of the Royal Society B-Biological Sciences 281.

Bengston SE, Jandt JM, 2014b. The development of collective personality: the ontogenetic drivers of behavioral variation across groups. Frontiers in Ecology and Evolution 2.

Bengston SE, Pruitt JN, Riechert SE, 2014. Differences in environmental enrichment generate contrasting behavioural syndromes in a basal spider lineage. Animal Behaviour 93:105-110.

Berryman AA, 1992. The origins and evolution of predator-prey theory. Ecology 73:1530-1535.

Beshers SN, Fewell J. N. , 2001. Models of division of labor in social insects. Annual Review in Entomology 46:413-440.

Beshers SN, Fewell JH, 2001. Models of division of labor in social insects. Annual Review of Entomology 46:413-440.

Beshers SN, Huang ZY, Oono Y, Robinson GE, 2001. Social inhibition and the regulation of temporal polyethism in honey bees. Journal of Theoretical Biology 213:461-479.

Bignell DE, Roisin Y, Lo N, 2011. Biology of Termites: A Modern Synthesis. Biology of Termites: a Modern Synthesis:1-576.

Bitterman ME, Menzel R, Fietz A, Schafer S, 1983. Classical-conditioning of proboscis extension in honeybees (Apis-mellifera). Journal of Comparative Psychology 97:107-119.

Blanchard GB, Orledge GM, Reynolds SE, Franks NR, 2000. Division of labour and seasonality in the ant Leptothorax albipennis: worker corpulence and its influence on behaviour. Animal Behaviour 59:723-738.

Blight O, Diaz-Mariblanca GA, Cerda X, Boulay R, 2016. A proactive-reactive syndrome affects group success in an ant species. Behavioral Ecology 27:118-125.

Blight O, Josens R, Bertelsmeier C, Abril S, Boulay R, Cerda X, 2017. Differences in behavioural traits among native and introduced colonies of an invasive ant. Biological Invasions 19:1389-1398.

Bockoven AA, Wilder SM, Eubanks MD, 2015. Intraspecific Variation among Social Insect Colonies: Persistent Regional and Colony-Level Differences in Fire Ant Foraging Behavior. Plos One 10.

Bologna MA, Bombi P, Pitzalis M, Turillazzi S, 2007. A previously unreported association between a social wasp and a social passerine bird. Tropical Zoology 20:211-214.

Bonabeau E, Theraulaz G, Deneubourg JL, 1998. Fixed response thresholds and the regulation of division of labor in insect societies. Bulletin of Mathematical Biology 60:753-807.

Bonabeau E, Theraulaz G, Deneubourg JL, Aron S, Camazine S, 1997. Self-organization in social insects. Trends in Ecology & Evolution 12:188-193.

Bourke AFG, 1999. Colony size, social complexity and reproductive conflict in social insects. Journal of Evolutionary Biology 12:245-257.

Breed MD, Guzman-Novoa E, Hunt GJ, 2004. Defensive behavior of honey bees: Organization, genetics, and comparisons with other bees. Annual Review of Entomology 49:271-298.

Breed MD, Rogers KB, 1991. The behavioral-genetics of colony defense in honeybees - genetic-variability for guarding behavior. Behavior Genetics 21:295-303.

Brodbeck FC, Greitemeyer T, 2000. Effects of individual versus mixed individual and group experience in rule induction on group member learning and group performance. Journal of Experimental Social Psychology 36:621-648.

Burns JG, Dyer AG, 2008. Diversity of speed-accuracy strategies benefits social insects. Curr Biol 18:R953-R954.

Camazine S, 1991. Self-organizing pattern-formation on the combs of honey-bee colonies. Behavioral Ecology and Sociobiology 28:61-76.

Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, Bonabeau E, 2001. Self-organization in biological systems. Self-organization in biological systems:i-viii, 1-538.

Carere C, Gherardi F, 2013. Animal personalities matter for biological invasions. Trends in Ecology & Evolution 28:5-6.

Carere C, Locurto C, 2011. Interaction between animal personality and animal cognition. Current Zoology 57:491-498.

Casey TM, Joos B, Fitzgerald TD, Yurlina ME, Young PA, 1988. Synchronized group foraging, thermoregulation, and growth of eastern tent caterpillars in relation to microclimate. Physiological Zoology 61:372-377.

Castellanos I, Barbosa P, 2006. Evaluation of predation risk by a caterpillar using substrate-borne vibrations. Animal Behaviour 72:461-469.

Cerda X, Arnan X, Retana J, 2013. Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology? Myrmecological News 18:131-147.

Chandra SBC, Hosler JS, Smith BH, 2000. Heritable variation for latent inhibition and its correlation with reversal learning in honeybees (Apis mellifera). Journal of Comparative Psychology 114:86-97.

Chang AT, Sih A, 2013. Multilevel selection and effects of keystone hyperaggressive males on mating success and behavior in stream water striders. Behav Ecol 24:1166-1176.

Chapman BB, Thain H, Coughlin J, Hughes WOH, 2011. Behavioural syndromes at multiple scales in Myrmica ants. Animal Behaviour 82:391-397.

Chapple DG, Simmonds SM, Wong BBM, 2012. Can behavioral and personality traits influence the success of unintentional species introductions? Trends in Ecology & Evolution 27:57-64.

Chittka L, Muller H, 2009. Learning, specialization, efficiency and task allocation in social insects. Communicative & Integrative Biology 2:151-154.

Chivers DP, Ferrari MCO, 2015. The effect of group size and tutor-to-observer ratio on socially learned antipredator responses in woodfrog tadpoles. Animal Behaviour 104:25-29.

Clark CW, Mangel M, 1986. THE EVOLUTIONARY ADVANTAGES OF GROUP FORAGING. Theoretical Population Biology 30:45-75.

Clinchy M, Sheriff MJ, Zanette LY, 2013. Predator-induced stress and the ecology of fear. Functional Ecology 27:56-65.

Cole BJ, 1983. Multiple mating and the evolution of social-behavior in the hymenoptera. Behavioral Ecology and Sociobiology 12:191-201.

Cole BJ, Edwards R, Holbrook CT, Holm L, Heyward J, Wiernasz DC, 2008. Does foraging activity affect foraging success in the western harvester ant (Hymenoptera : formicidae)? Annals of the Entomological Society of America 101:272-276.

Cole BJ, Smith AA, Huber ZJ, Wiernasz DC, 2010. The structure of foraging activity in colonies of the harvester ant, Pogonomyrmex occidentalis. Behavioral Ecology 21:337-342.

Collins AM, Rinderer TE, Harbo JR, Bolten AB, 1982. Colony defense by africanized and european honey bees. Science 218:72-74.

Conradt L, 2012. Models in animal collective decision-making: information uncertainty and conflicting preferences. Interface Focus 2:226-240.

Costa JT, Ross KG, 2003. Fitness effects of group merging in a social insect. Proceedings of the Royal Society B-Biological Sciences 270:1697-1702.

Cote J, Clobert J, Brodin T, Fogarty S, Sih A, 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. Philosophical Transactions of the Royal Society B-Biological Sciences 365:4065-4076.

Cote J, Fogarty S, Brodin T, Weinersmith K, Sih A, 2011. Personality-dependent dispersal in the invasive mosquitofish: group composition matters. Proc R Soc B-Biol Sci 278:1670-1678.

Cote J, Fogarty S, Tymen B, Sih A, Brodin T, 2013. Personality-dependent dispersal cancelled under predation risk. Proceedings of the Royal Society B-Biological Sciences 280.

Couzin ID, Krause J, Franks NR, Levin SA, 2005. Effective leadership and decision-making in animal groups on the move. Nature 433:513-516.

Crane AL, Mathiron AGE, Ferrari MCO, 2015. Social learning in a high-risk environment: incomplete disregard for the 'minnow that cried pike' results in culturally transmitted neophobia. Proceedings of the Royal Society B-Biological Sciences 282:216-223.

Daly M, Behrends PR, Wilson MI, Jacobs LF, 1992. Behavioral modulation of predation risk - moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, Dipodomys merriami. Animal Behaviour 44:1-9.

Darwin C, 1859. On the origins of species by means of natural selection. London: Murray.

David M, Salignon M, Perrot-Minnot MJ, 2014. Shaping the antipredator strategy: flexibility, consistency, and behavioral correlations under varying predation threat. Behavioral Ecology 25:1148-1156.

Davidson DW, 1998. Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. Ecological Entomology 23:484-490.

Dehn MM, 1990. Vigilance for predators - detection and dilution effects. Behavioral Ecology and Sociobiology 26:337-342.

Deneubourg JL, Aron S, Goss S, Pasteels JM, 1990. The self-organizing exploratory pattern of the Argentine ant. Journal of Insect Behavior 3:159-168.

Detrain C, Deneubourg JL, 2008. Collective Decision-Making and Foraging Patterns in Ants and Honeybees. Advances in Insect Physiology, Vol 35 35:123-173.

Dingemanse NJ, Kazem AJN, Reale D, Wright J, 2010. Behavioural reaction norms: animal personality meets individual plasticity. Trends Ecol Evol 25:81-89.

DiRienzo N, Dornhaus A, 2017. Temnothorax rugatulus ant colonies consistently vary in nest structure across time and context. Plos One 12.

Doering GN, Pratt SC, 2016. Queen location and nest site preference influence colony reunification by the ant Temnothorax rugatulus. Insectes Sociaux 63:585-591.

Donahoe K, Lewis LA, Schneider SS, 2003. The role of the vibration signal in the house-hunting process of honey bee (Apis mellifera) swarms. Behavioral Ecology and Sociobiology 54:593-600.

Dornhaus A, Holley JA, Pook VG, Worswick G, Franks NR, 2008. Why do not all workers work? Colony size and workload during emigrations in the ant Temnothorax albipennis. Behavioral Ecology and Sociobiology 63:43-51.

Dornhaus A, Powell S, Bengston S, 2012. Group Size and Its Effects on Collective Organization. Annual Review of Entomology, Vol 57 57:123-141.

Dostalkova I, Spinka M, 2007. Synchronization of behaviour in pairs: the role of communication and consequences in timing. Animal Behaviour 74:1735-1742.

Downes S, 2001. Trading heat and food for safety: Costs of predator avoidance in a lizard. Ecology 82:2870-2881.

Downs SG, Ratnieks FLW, 2000. Adaptive shifts in honey bee (Apis mellifera L.) guarding behavior support predictions of the acceptance threshold model. Behavioral Ecology 11:326-333.

Dumke M, Herberstein ME, Schneider JM, 2016. Producers and scroungers: feeding-type composition changes with group size in a socially foraging spider. Proceedings of the Royal Society B-Biological Sciences 283.

Dyer JRG, Croft DP, Morrell LJ, Krause J, 2009. Shoal composition determines foraging success in the guppy. Behav Ecol 20:165-171.

Ebert D, 1998. Behavioral asymmetry in relation to body weight and hunger in the tropical social spider Anelosimus eximius (Araneae, Theridiidae). Journal of Arachnology 26:70-80.

Eisner T, Kriston I, Aneshansley DJ, 1976. Defense-mechanisms of arthropods .47. Defensive behavior of a termite (Nasutitermes-exitiosus). Behavioral Ecology and Sociobiology 1:83-125.

Elgar MA, 1989. Predator vigilance and group-size in mammals and birds - a critical review of the empirical evidence. Biological Reviews of the Cambridge Philosophical Society 64:13-33.

Evans LJ, Raine NE, 2014. Changes in Learning and Foraging Behaviour within Developing Bumble Bee (Bombus terrestris) Colonies. Plos One 9.

Fahrbach SE, Robinson GE, 1996. Juvenile hormone, behavioral maturation, and brain structure in the honey bee. Developmental Neuroscience 18:102-114.

Fennessy PF, 1984. Red deer—behaviour and ecology of two sexes. Journal of the Royal Society of New Zealand 14:289-290.

Ferkin MH, Combs A, delBarco-Trillo J, Pierce AA, Franklin S, 2008. Meadow voles, Microtus pennsylvanicus, have the capacity to recall the "what", "where", and "when" of a single past event. Anim Cogn 11:147-159.

Fitzgerald TD, Costa JT, 1986. Trail-based communication and foraging behavior of young colonies of forest tent caterpillars (Lepidoptera, lasiocampidae). Annals of the Entomological Society of America 79:999-1007.

Fitzgerald TD, Peterson SC, 1988. Cooperative foraging and communication in caterpillars. Bioscience 38:20-25.

Flack JC, Girvan M, de Waal FBM, Krakauer DC, 2006. Policing stabilizes construction of social niches in primates. Nature 439:426-429.

Foley C, Pettorelli N, Foley L, 2008. Severe drought and calf survival in elephants. Biology Lett 4:541-544.

Foster WA, Treherne JE, 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. Nature 293:466-467.

Franks N, Tofts C, 1994. Foraging for work: how tasks allocate workers. Animal Behaviour. p. 470-472.

Franks NR, Dechaume-Moncharmont FX, Hanmore E, Reynolds JK, 2009. Speed versus accuracy in decision-making ants: expediting politics and policy implementation. Philos T R Soc B 364:845-852.

Frost EH, Shutler D, Hillier NK, 2013. Effects of fluvalinate on honey bee learning, memory, responsiveness to sucrose, and survival. Journal of Experimental Biology 216:2931-2938.

Furuichi S, Kasuya E, 2014. Costs, benefits, and plasticity of construction of nest defensive structures in paper wasps. Behav Ecol Sociobiol 68:215-221.

Galef BG, Laland KN, 2005. Social learning in animals: Empirical studies and theoretical models. Bioscience 55:489-499.

Gautrais J, Theraulaz G, Deneubourg JL, Anderson C, 2002. Emergent polyethism as a consequence of increased colony size in insect societies. Journal of Theoretical Biology 215:363-373.

Gilbert C, Robertson G, Le Maho Y, Naito Y, Ancel A, 2006. Huddling behavior in emperor penguins: Dynamics of huddling. Physiology & Behavior 88:479-488.

Gill RJ, Ramos-Rodriguez O, Raine NE, 2012. Combined pesticide exposure severely affects individual- and colony-level traits in bees. Nature 491:105-U119.

Gordon DM, 1986. The dynamics of the daily round of the harvester ant colony (pogonomyrmex-barbatus). Animal Behaviour 34:1402-1419.

Gordon DM, 1989. Dynamics of task switching in harvester ants. Animal Behaviour 38:194-204.

Gordon DM, 1996. The organization of work in social insect colonies. Nature 380:121-124.

Gordon DM, 2013a. The rewards of restraint in the collective regulation of foraging by harvester ant colonies. Nature.

Gordon DM, 2013b. The rewards of restraint in the collective regulation of foraging by harvester ant colonies. Nature 498:91-+.

Gordon DM, Dektar KN, Pinter-Wollman N, 2013. Harvester Ant Colony Variation in Foraging Activity and Response to Humidity. Plos One 8.

Gordon DM, Guetz A, Greene MJ, Holmes S, 2011. Colony variation in the collective regulation of foraging by harvester ants. Behavioral Ecology 22:429-435.

Griffin AS, 2004. Social learning about predators: A review and prospectus. Learning & Behavior 32:131-140.

Griffin AS, Guillette LM, Healy SD, 2015. Cognition and personality: an analysis of an emerging field. Trends in Ecology & Evolution 30:207-214.

Grinsted L, Bacon JP, 2014. Animal Behaviour: Task Differentiation by Personality in Spider Groups. Current Biology 24:R749-R751.

Grinsted L, Pruitt JN, Settepani V, Bilde T, 2013. Individual personalities shape task differentiation in a social spider. Proceedings of the Royal Society B-Biological Sciences 280.

Guzman-Novoa E, Hunt GJ, Uribe-Rubio JL, Prieto-Merlos D, 2004. Genotypic effects of honey bee (Apis mellifera) defensive behavior at the individual and colony levels: the relationship of guarding, pursuing and stinging. Apidologie 35:15-24.

Hamilton WD, 1964. Genetical evolution of social behaviour I. Journal of Theoretical Biology 7:1-&.

Hamilton WD, 1971. Geometry for selfish herd. Journal of Theoretical Biology 31:295.

Harvey JA, Corley LS, Strand MR, 2000. Competition induces adaptive shifts in caste ratios of a polyembryonic wasp. Nature 406:183-186.

Harwood G, Aviles L, 2013. Differences in group size and the extent of individual participation in group hunting may contribute to differential prey-size use among social spiders. Biology Letters 9.

Hasegawa E, 1997. The optimal caste ratio in polymorphic ants: Estimation and empirical evidence. American Naturalist 149:706-722.

Henschel JR, 1998. Predation on social and solitary individuals of the spider Stegodyphus dumicola (Araneae, Eresidae). Journal of Arachnology 26:61-69.

Herbers JM, 1980. On caste ratios in ant colonies - population responses to changing environments. Evolution 34:575-585.

Herberstein ME, Hebets E, Penney D, 2013. Why are spiders good models for research? In: Penney D, editor. Spider Research in the 21st Century: Trends & Perspectives. p. 230-251.

Hermann HR, Blum MS, 1981. Defensive mechanisms in the social Hymenoptera. Social insects Volume 2:77-197.

Heyes CM, Galef BG, 1996. Social learning in animals: the roots of culture. Elsevier.

Hobaiter C, Poisot T, Zuberbuhler K, Hoppitt W, Gruber T, 2014. Social Network Analysis Shows Direct Evidence for Social Transmission of Tool Use in Wild Chimpanzees. Plos Biology 12.

Holbrook CT, Barden PM, Fewell JH, 2011. Division of labor increases with colony size in the harvester ant Pogonomyrmex californicus. Behavioral Ecology 22:960-966.

Holbrook CT, Wright CM, Pruitt JN, 2014. Individual differences in personality and behavioural plasticity facilitate division of labour in social spider colonies. Anim Behav 97:177-183.

Holldobler B, Wilson EO, 1990. The ants. Cambridge, MA: Belknap Press.

Huang ZY, Robinson GE, 1992. Honeybee colony integration - worker worker interactions mediate hormonally regulated plasticity in division-of-labor. Proceedings of the National Academy of Sciences of the United States of America 89:11726-11729.

Huang ZY, Robinson GE, 1996. Regulation of honey bee division of labor by colony age demography. Behavioral Ecology and Sociobiology 39:147-158.

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.

Hunt GJ, 2007. Flight and fight: A comparative view of the neurophysiology and genetics of honey bee defensive behavior. Journal of Insect Physiology 53:399-410.

Hölldobler B, Wilson EO, 2009. The superorganism: the beauty, elegance, and strangeness of insect societies: WW Norton & Company.

Ingram KK, Oefner P, Gordon DM, 2005. Task-specific expression of the foraging gene in harvester ants. Molecular Ecology 14:813-818.

Ings TC, Raine NE, Chittka L, 2009. A population comparison of the strength and persistence of innate colour preference and learning speed in the bumblebee Bombus terrestris. Behavioral Ecology and Sociobiology 63:1207-1218.

Itani J, 1958. On the acquisition and propagation of a new food habit in the natural group of the Japanese monkey at Takasaki-Yama. Primates 1:84-98.

Jackson RR, Cross FR, 2011. Spider Cognition. Advances in Insect Physiology, Vol 41: Spider Physiology and Behaviour - Behaviour 41:115-174.

Jakob E, Skow CD, Long SM, 2011. Plasticity, learning and cognition. In: Herberstein ME, editor. Spider Behavior: Flexibility and Versatility Cambridge.

Jakob EM, Marshall SD, Uetz GW, 1996. Estimating fitness: A comparison of body condition indices. Oikos 77:61-67.

Jandt JM, Bengston S, Pinter-Wollman N, Pruitt JN, Raine NE, Dornhaus A, Sih A, 2014. Behavioral syndromes and social insects: Multiple levels of personality. Biological Reviews 89:48-67.

Jandt JM, Bengston S, Pinter-Wollman N, Pruitt JN, Raine NE, Dornhaus A, Sih A, 2013. Behavioural syndromes and social insects: personality at multiple levels. Biological Reviews.

Jandt JM, Dornhaus A, 2009. Spatial organization and division of labour in the bumblebee Bombus impatiens. Animal Behaviour 77:641-651.

Jandt JM, Gordon DM, 2016. The behavioral ecology of variation in social insects. Current Opinion in Insect Science 15:40-44.

Jandt JM, Huang E, Dornhaus A, 2009. Weak specialization of workers inside a bumble bee (Bombus impatiens) nest. Behavioral Ecology and Sociobiology 63:1829-1836.

Jandt JM, Sarah Bengston, Noa Pinter-Wollman, Jonathan N. Pruitt, Nigel E. Raine, Anna Dornhaus, and Andrew Sih, 2013. Behavioural syndromes and social insects: personality at multiple levels. Biological Reviews.

Jeanne RL, 1986. The organization of work in Polybia occidentalis - costs and benefits of specialization in a social wasp. Behavioral Ecology and Sociobiology 19:333-341.

Jeanson R, Fewell JH, 2008. Influence of the social context on division of labor in ant foundress associations. Behavioral Ecology 19:567-574.

Johnson CJ, Sih A, 2005. Precopulatory sexual cannibalism in fishing spiders (Dolomedes triton): a role for behavioral syndromes. Behavioral Ecology and Sociobiology 58:390-396.

Jolles JW, Fleetwood-Wilson A, Nakayama S, Stumpe MC, Johnstone RA, Manica A, 2015. The role of social attraction and its link with boldness in the collective movements of three-spined sticklebacks. Animal Behaviour 99:147-153.

Jones JC, Oldroyd BP, 2007. Nest thermoregulation in social insects. Advances in Insect Physiology, Vol 33 33:153-191.

Judd TM, 1998. Defensive behavior of colonies of the paper wasp, Polistes fuscatus, against vertebrate predators over the colony cycle. Insectes Soc 45:197-208.

Karsai I, Penzes Z, 1993. Comb building in social wasps - self-organization and stigmergic script. Journal of Theoretical Biology 161:505-525.

Keiser CN, Howell KA, Pinter-Wollman N, Pruitt JN, 2016a. Personality composition alters the transmission of cuticular bacteria in social groups. Biology Letters 12.

Keiser CN, Jones DK, Modlmeier AP, Pruitt JN, 2014a. Exploring the effects of individual traits and within-colony variation on task differentiation and collective behavior in a desert social spider. Behav Ecol Sociobiol 68:839-850.

Keiser CN, Jones DK, Modlmeier AP, Pruitt JN, 2014b. Exploring the effects of individual traits and within-colony variation on task differentiation and collective behavior in a desert social spider. Behavioral Ecology and Sociobiology 68:839-850.

Keiser CN, Modlmeier AP, Singh N, Jones DK, Pruitt JN, 2014c. Exploring How a Shift in the Physical Environment Shapes Individual and Group Behavior across Two Social Contexts. Ethology 120:825-833.

Keiser CN, Pinter-Wollman N, Augustine DA, Ziemba MJ, Hao LR, Lawrence JG, Pruitt JN, 2016b. Individual differences in boldness influence patterns of social interactions and the transmission of cuticular bacteria among group-mates. Proceedings of the Royal Society B-Biological Sciences 283.

Keiser CN, Pinter-Wollman N, Ziemba MJ, Kothamasu KS, Pruitt JN, 2017. The index case is not enough: Variation among individuals, groups, and social networks modify bacterial transmission dynamics. Journal of Animal Ecology.

Keiser CN, Pruitt JN, 2014. Personality composition is more important than group size in determining collective foraging behaviour in the wild. Proceedings of the Royal Society B.

Keiser CN, Vojvodic S, Butler IO, Sartain E, Rudolf VHW, Saltz JB, 2018. Queen presence mediates the relationship between collective behaviour and disease susceptibility in ant colonies. Journal of Animal Ecology 87:379-387.

Keiser CN, Wright CM, Pruitt JN, 2015a. Warring arthropod societies: Colony apparency and group size jointly dictate the survivorship of social spiders in a predator-dense habitat.

Keiser CN, Wright CM, Pruitt JN, 2015b. Warring arthropod societies: Social spider colonies can delay annihilation by predatory ants via reduced apparency and increased group size. Behavioural processes 119:14-21.

Keiser CN, Wright CM, Pruitt JN, 2016c. Increased bacterial load can reduce or negate the effects of keystone individuals on group collective behaviour. Animal Behaviour 114:211-218.

Keiser CN, Wright CM, Singh N, DeShane JA, Modlmeier AP, Pruitt JN, 2015c. Cross-fostering by foreign conspecific queens and slave-making workers influences individual- and colony-level personality. Behavioral Ecology and Sociobiology 69:395-405.

Keller L, Ross KG, 1998. Selfish genes: a green beard in the red fire ant. Nature 394:573-575.

Kerth G, 2008. Causes and consequences of sociality in bats. Bioscience 58:737-746.

Kerth G, Ebert C, Schmidtke C, 2006. Group decision making in fission-fusion societies: evidence from two-field experiments in Bechstein's bats. Proceedings of the Royal Society B-Biological Sciences 273:2785-2790.

Kim K, Krafft B, Choe J, 2005. Cooperative prey capture by young subsocial spiders: II. Behavioral mechanism. Behavioral Ecology and Sociobiology 59:101-107.

King AJ, Douglas CMS, Huchard E, Isaac NJB, Cowlishaw G, 2008. Dominance and Affiliation Mediate Despotism in a Social Primate. Current Biology 18:1833-1838.

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.

Knoernschild M, Nagy M, Metz M, Mayer F, von Helversen O, 2010. Complex vocal imitation during ontogeny in a bat. Biology Letters 6:156-159.

Koolhaas JM, de Boer SF, Buwalda B, van Reenen K, 2007. Individual variation in coping with stress: A multidimensional approach of ultimate and proximate mechanisms. Brain Behav Evol 70:218-226.

Kralj J, Brockmann A, Fuchs S, Tautz J, 2007. The parasitic mite Varroa destructor affects non-associative learning in honey bee foragers, Apis mellifera L. Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology 193:363-370.

Krause J, 1994. Differential fitness returns in relation to spatial position in groups. Biological Reviews of the Cambridge Philosophical Society 69:187-206.

Krause J, Bumann D, Todt D, 1992. Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (Rutilus-rutilus). Behavioral Ecology and Sociobiology 30:177-180.

Krause J, Godin JGJ, 1995. Predator preferences for attacking particular prey group sizes - consequences for predator hunting success and prey predation risk. Animal Behaviour 50:465-473.

Krause J, Ruxton GD, 2002. Living in groups: Oxford University Press.

Krause J, Ruxton GD, Krause S, 2010. Swarm intelligence in animals and humans. Trends Ecol Evol 25:28-34.

Kronauer DJC, Schoning C, Pedersen JS, Boomsma JJ, Gadau J, 2004. Extreme queen-mating frequency and colony fission in African army ants. Molecular Ecology 13:2381-2388. Kullmann EJ, 1972. Evolution of social behavior in spiders (Araneae - Eresidae and Theridiidae). American Zoologist 12:419.

Laland KN, Williams K, 1998. Social transmission of maladaptive information in the guppy. Behavioral Ecology 9:493-499.

Laskowski KL, Montiglio P, Pruitt JN, 2016a. Individual and group performance suffers from social niche disruption. American Naturalist 187.

Laskowski KL, Montiglio PO, Pruitt JN, 2016b. Individual and Group Performance Suffers from Social Niche Disruption. American Naturalist 187:776-785.

Laskowski KL, Montiglio PO, Pruitt JN, in review. Individual and group performance suffers from social niche disruption. Proceedings of the National Academy of Sciences.

Laskowski KL, Pruitt JN, 2014a. Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider. Proc R Soc B-Biol Sci 281:20133166.

Laskowski KL, Pruitt JN, 2014b. Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider. Proceedings of the Royal Society B-Biological Sciences 281.

Lefebvre L, 1995. The opening of milk bottles by birds: evidence for accelerating learning rates, but against the wave-of-advance model of cultural transmission. Behavioural Processes 34:43-53.

Lefevre T, Adamo SA, Biron DG, Misse D, Hughes D, Thomas F, 2009. Invasion of the Body Snatchers: The Diversity and Evolution of Manipulative Strategies in Host-Parasite Interactions. Advances in Parasitology, Vol 68: Natural History of Host-Parasite Interactions 68:45-+.

Lichtenstein JL, Pruitt JN, Modlmeier AP, 2015. Intraspecific variation in collective behaviors drives interspecific contests in acorn ants.1-7.

Lichtenstein JLL, Pruitt JN, Modlmeier AP, 2016a. Intraspecific variation in collective behaviors drives interspecific contests in acorn ants. Behavioral Ecology 27:553-559.

Lichtenstein JLL, Wright CM, Luscuskie LP, Montgomery GA, Pinter-Wollman N, Pruitt JN, 2016b. Participation in cooperative prey capture and the benefits gained from it are associated with individual personality. Current Zoology.

Lima SL, 1995. Back to the basics of antipredatory vigilance - the group-size effect. Animal Behaviour 49:11-20.

Lima SL, 1998. Nonlethal effects in the ecology of predator-prey interactions - What are the ecological effects of anti-predator decision-making? Bioscience 48:25-34.

Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation - a review and prospectus. Canadian Journal of Zoology-Revue Canadienne De Zoologie 68:619-640.

List C, Elsholtz C, Seeley TD, 2009. Independence and interdependence in collective decision making: an agent-based model of nest-site choice by honeybee swarms. Philosophical Transactions of the Royal Society B-Biological Sciences 364:755-762.

Lohrey AK, Clark DL, Gordon SD, Uetz GW, 2009. Antipredator responses of wolf spiders (Araneae: Lycosidae) to sensory cues representing an avian predator. Animal Behaviour 77:813-821.

Lubin Y, 1995. Is there division-of-labor in the social spider achaearanea wau (Theridiidae). Animal Behaviour 49:1315-1323.

Lubin Y, Bilde T, 2007. The evolution of sociality in spiders. Advances in the Study of Behavior, Vol 37 37:83-145.

Mallon EB, Pratt SC, Franks NR, 2001. Individual and collective decision-making during nest site selection by the ant Leptothorax albipennis. Behavioral Ecology and Sociobiology 50:352-359.

Mappes J, Marples N, Endler JA, 2005. The complex business of survival by aposematism. Trends Ecol Evol 20:598-603.

Marting PR, Wcislo WT, Pratt SC, 2018. Colony personality and plant health in the Azteca-Cecropia mutualism. Behavioral Ecology 29:264-271.

McComb K, Shannon G, Durant SM, Sayialel K, Slotow R, Poole J, Moss C, 2011. Leadership in elephants: the adaptive value of age. P R Soc B 278:3270-3276.

Merilaita S, Tuomi J, Jormalainen V, 1999. Optimization of cryptic coloration in heterogeneous habitats. Biol J Linn Soc 67:151-161.

Mizumoto N, Kobayashi K, Matsuura K, 2015. Emergence of intercolonial variation in termite shelter tube patterns and prediction of its underlying mechanism. Royal Society Open Science 2.

Mizumoto N, Matsuura K, 2013. Colony-specific architecture of shelter tubes by termites. Insectes Sociaux 60:525-530.

Modlmeier A, Keiser C, Shearer T, Pruitt J, 2014a. Species-specific influence of group composition on collective behaviors in ants. Behavioral Ecology and Sociobiology.

Modlmeier AP, Foitzik S, 2011. Productivity increases with variation in aggression among group members in Temnothorax ants. Behavioral Ecology 22:1026-1032.

Modlmeier AP, Forrester NJ, Pruitt JN, 2014b. Habitat structure helps guide the emergence of colony-level personality in social spiders. Behavioral Ecology and Sociobiology.

Modlmeier AP, Keiser CN, Shearer TA, Pruitt JN, 2014c. Species-specific influence of group composition on collective behaviors in ants. Behavioral Ecology and Sociobiology 68:1929-1937.

Modlmeier AP, Keiser CN, Watters JV, Sih A, Pruitt JN, 2014d. The keystone individual concept: an ecological and evolutionary overview. Animal Behaviour 89:53-62.

Modlmeier AP, Keiser CN, Wright CM, Lichtenstein JLL, Pruitt JN, 2015a. Integrating animal personality into insect population and community ecology. Current Opinion in Insect Science: Elsevier. p. 77-85.

Modlmeier AP, Laskowski KL, Brittingham HA, Coleman A, Knutson KA, Kuo C, McGuirk M, Zhao K, Keiser CN, Pruitt JN, 2015b. Adult presence augments juvenile collective foraging in social spiders. Animal Behaviour 109:9-14.

Modlmeier AP, Laskowski KL, DeMarco AE, Coleman A, Zhao K, Brittingham HA, McDermott DR, Pruitt JN, 2014e. Persistent social interactions beget more pronounced personalities in a desert-dwelling social spider. Biology Letters. p. 2014-2019.

Modlmeier AP, Laskowski KL, DeMarco AE, Coleman A, Zhao K, Brittingham HA, McDermott DR, Pruitt JN, 2014f. Persistent social interactions beget more pronounced personalities in a desert-dwelling social spider. Biology Letters. p. 2014-2019.

Modlmeier AP, Liebmann JE, Foitzik S, 2012. Diverse societies are more productive: a lesson from ants. Proc Biol Sci 279:2142-2150.

Moore AJ, Brodie ED, Wolf JB, 1997. Interacting phenotypes and the evolutionary process .1. Direct and indirect genetic effects of social interactions. Evolution 51:1352-1362.

Muratori FB, Rouyar A, Hance T, 2014. Clonal variation in aggregation and defensive behavior in pea aphids. Behavioral Ecology 25:901-908.

Murdoch WW, Briggs CJ, Nisbet RM, 2003. Consumer-resource dynamics: Princeton University Press.

Nentwig W, 1985. Social spiders catch larger prey - a study of Anelosimus eximius (Araneae, Theridiidae). Behavioral Ecology and Sociobiology 17:79-85.

Nerniroff L, Despland E, 2007. Consistent individual differences in the foraging behaviour of forest tent caterpillars (Malacosoma disstria). Canadian Journal of Zoology-Revue Canadienne De Zoologie 85:1117-1124.

Niemela PT, Vainikka A, Lahdenpera S, Kortet R, 2012. Nymphal density, behavioral development, and life history in a field cricket. Behavioral Ecology and Sociobiology 66:645-652.

Nonacs P, Blumstein DT, 2010. Predation risk and behavioral life history. Evolutionary behavioral ecology:207-221.

Nonacs P, Dill LM, 1990. Mortality risk vs food quality trade-offs in a common currency - ant patch preferences. Ecology 71:1886-1892.

Nonacs P, Dill LM, 1991. Mortality risk versus food quality trade-offs in ants - patch use over time. Ecol Entomol 16:73-80.

Nonacs P, Kapheim KM, 2007. Social heterosis and the maintenance of genetic diversity. Journal of Evolutionary Biology 20:2253-2265.

Nonacs P, Kapheim KM, 2008. Social heterosis and the maintenance of genetic diversity at the genome level. Journal of Evolutionary Biology 21:631-635.

Norman VC, Pamminger T, Hughes WOH, 2017. The effects of disturbance threat on leaf-cutting ant colonies: a laboratory study. Insectes Sociaux 64:75-85.

Nowak MA, Tarnita CE, Wilson EO, 2010. The evolution of eusociality. Nature 466:1057-1062.

Oldroyd BP, Fewell JH, 2007. Genetic diversity promotes homeostasis in insect colonies. Trends Ecol Evol 22:408-413.

Oliveira RF, 2009. Social behavior in context: Hormonal modulation of behavioral plasticity and social competence. Integrative and Comparative Biology 49:423-440.

Orrock JL, Grabowski JH, Pantel JH, Peacor SD, Peckarsky BL, Sih A, Werner EE, 2008. Consumptive and nonconsumptive effects of predators on metacommunities of competing prey. Ecology 89:2426-2435.

Oster G, Wilson EO, 1978. Castes and Ecology in the Social Insects. Princeton, NJ: Princeton University Press.

Oster G, Wilson, E. O., 1978. Castes and Ecology in the Social Insects. Princeton, NJ: Princeton University Press.

Pacala SW, Gordon DM, Godfray HCJ, 1996. Effects of social group size on information transfer and task allocation. Evol Ecol 10:127-165.

Page RE, Erber J, Fondrk MK, 1998. The effect of genotype on response thresholds to sucrose and foraging behavior of honey bees (Apis mellifera L.). Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology 182:489-500.

Page RE, Robinson GE, 1991. The genetics of division-of-labor in honey-bee colonies. Advances in Insect Physiology 23:117-169.

Paleolog J, 2009. Behavioural characteristics of honey bee (Apis mellifera) colonies containing mix of workers of divergent behavioural traits. Animal Science Papers and Reports 27:237-248.

Pamminger T, Scharf I, Pennings PS, Foitzik S, 2011. Increased host aggression as an induced defense against slave-making ants. Behavioral Ecology 22:255-260.

Pankiw T, 2003. Directional change in a suite of foraging behaviors in tropical and temperate evolved honey bees (Apis mellifera L.). Behavioral Ecology and Sociobiology 54:458-464.

Pankiw T, Page RE, 1999. The effect of genotype, age, sex, and caste on response thresholds to sucrose and foraging behavior of honey bees (Apis mellifera L.). Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology 185:207-213.

Pankiw T, Page RE, 2003. Effect of pheromones, hormones, and handling on sucrose response thresholds of honey bees (Apis mellifera L.). Journal of Comparative

Physiology a-Neuroethology Sensory Neural and Behavioral Physiology 189:675-684.

Pankiw T, Page RE, Fondrk MK, 1998. Brood pheromone stimulates pollen foraging in honey bees (Apis mellifera). Behavioral Ecology and Sociobiology 44:193-198.

Pankiw T, Waddington KD, Page RE, 2001. Modulation of sucrose response thresholds in honey bees (Apis mellifera L.): influence of genotype, feeding, and foraging experience. Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology 187:293-301.

Parr CL, 2008. Dominant ants can control assemblage species richness in a South African savanna. Journal of Animal Ecology 77:1191-1198.

Pasquier G, Gruter C, 2016. Individual learning performance and exploratory activity are linked to colony foraging success in a mass-recruiting ant. Behavioral Ecology 27:1702-1709.

Passino KM, Seeley TD, Visscher PK, 2008. Swarm cognition in honey bees. Behavioral Ecology and Sociobiology 62:401-414.

Pearce AN, Huang ZY, Breed MD, 2001. Juvenile hormone and aggression in honey bees. Journal of Insect Physiology 47:1243-1247.

Peckmezian T, Taylor PW, 2015. A virtual reality paradigm for the study of visually mediated behaviour and cognition in spiders. Animal Behaviour 107:87-95.

Perez-Tris J, Diaz JA, Telleria JL, 2004. Loss of body mass under predation risk: cost of antipredatory behaviour or adaptive fit-for-escape? Animal Behaviour 67:511-521.

Perkins TA, Riechert SE, Jones TC, 2007. Interactions between the social spider Anelosimus studiosus (Araneae, Theridiidae) and foreign spiders that frequent its nests. Journal of Arachnology 35:143-152.

Pescetta M, Spiezio C, Grassi D, Previde EP, 2008. Spread of new tool-use behaviour in captive chimpanzees: Observational learning. Folia Primatologica 79:145-146.

Pinter-Wollman N, 2012. Personality in social insects: How does worker personality determine colony personality? Current Zoology 58:580-588.

Pinter-Wollman N, 2015. Nest architecture shapes the collective behaviour of harvester ants. Biology Letters 11.

Pinter-Wollman N, Gordon DM, Holmes S, 2012. Nest site and weather affect the personality of harvester ant colonies. Behavioral Ecology 23:1022-1029.

Pinter-Wollman N, Mi, Brian, Pruitt JN, 2017. Replacing bold individuals has a smaller impact on group performance than replacing shy individuals. Behavioral Ecology.

Planas-Sitja I, Deneubourg JL, Gibon C, Sempo G, 2015. Group personality during collective decision-making: a multi-level approach. Proceedings of the Royal Society B-Biological Sciences 282.

Powers KS, Aviles L, 2007. The role of prey size and abundance in the geographical distribution of spider sociality. Journal of Animal Ecology 76:995-1003.

Pratt SC, Mallon EB, Sumpter DJT, Franks NR, 2002. Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant Leptothorax albipennis. Behavioral Ecology and Sociobiology 52:117-127.

Preisser EL, Bolnick DI, Benard MF, 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86:501-509.

Pruitt JN, 2012. Behavioural traits of colony founders affect the life history of their colonies. Ecology Letters 15:1026-1032.

Pruitt JN, 2013. A real-time eco-evolutionary dead-end strategy is mediated by the traits of lineage progenitors and interactions with colony invaders. Ecology Letters 16:879-886.

Pruitt JN, Avilés L, 2017. Social spiders: mildly successful social animals with much untapped research potential. Animal Behaviour.

Pruitt JN, Cote J, Ferrari MCO, 2012a. Behavioural trait variants in a habitat-forming species dictate the nature of its interactions with and among heterospecifics. Functional Ecology 26:29-36.

Pruitt JN, Ferrari MCO, 2011. Intraspecific trait variants determine the nature of interspecific interactions in a habitat-forming species. Ecology 92:1902-1908.

Pruitt JN, Goodnight CJ, 2014. Site-specific group selection drives locally adapted colony compositions. Nature.

Pruitt JN, Goodnight CJ, Riechert SE, 2017a. Intense group selection selects for ideal group compositions, but selection within groups maintains them. Animal Behaviour 124:15-24.

Pruitt JN, Goodnight, C. J., 2014. Site-specific group selection drives locally adapted colony compositions. Nature.

Pruitt JN, Grinsted L, Settepani V, 2013. Linking levels of personality: personalities of the 'average' and 'most extreme' group members predict colony-level personality. Animal Behaviour 86:391-399.

Pruitt JN, Iturralde G, Aviles L, Riechert SE, 2011. Amazonian social spiders share similar within-colony behavioural variation and behavioural syndromes. Animal Behaviour 82:1449-1455.

Pruitt JN, Keiser CN, 2014a. The personality types of key catalytic individuals shape colonies' collective behaviour and success. Animal Behaviour 93:87-95.

Pruitt JN, Keiser CN, 2014b. The personality types of key catalytic individuals shape colonies' collective behaviour and success. Anim Behav 93:87–95.

Pruitt JN, Oufiero CE, Aviles L, Riechert SE, 2012b. Iterative Evolution of Increased Behavioral Variation Characterizes the Transition to Sociality in Spiders and Proves Advantageous. American Naturalist 180:496-510.

Pruitt JN, Pinter-wollman N, 2015. The legacy effects of keystone individuals on collecitve behavior scale to how long they remain within a group. Proc R Soc B-Biol Sci.

Pruitt JN, Pinter-Wollman N, 2015. The legacy effects of keystone individuals on collective behaviour scale to how long they remain within a group. Proceedings of the Royal Society B-Biological Sciences 282:89-96.

Pruitt JN, Riechert SE, 2009. Frequency-dependent success of cheaters during foraging bouts might limit their spread within colonies of a socially polymorphic spider. Evolution 63:2966-2973.

Pruitt JN, Riechert SE, 2011a. How within-group behavioural variation and task efficiency enhance fitness in a social group. Proceedings of the Royal Society B-Biological Sciences 278:1209-1215.

Pruitt JN, Riechert SE, 2011b. Within-group behavioral variation promotes biased task performance and the emergence of a defensive caste in a social spider. Behavioral Ecology and Sociobiology 65:1055-1060.

Pruitt JN, Riechert SE, Jones TC, 2008. Behavioural syndromes and their fitness consequences in a socially polymorphic spider, Anelosimus studiosus. Animal Behaviour 76:871-879.

Pruitt JN, Wright CM, Keiser CN, DeMarco AE, Grobis MM, Pinter-Wollman N, 2016. The Achilles' heel hypothesis: misinformed keystone individuals impair collective learning and reduce group success. Proceedings of the Royal Society B-Biological Sciences 283.

Pruitt JN, Wright CM, Lichtenstein JLL, Chism GT, McEwen BL, Kamath A, Pinter-Wollman N, 2017b. Selection for Collective Aggressiveness Favors Social Susceptibility in Social Spiders. Current Biology 28:100-105.

Raine NE, Chittka L, 2005. Colour preferences in relation to the foraging performance and fitness of the bumblebee Bombus terrestris. Uludag Bee Journal 5:145-150.

Raine NE, Chittka L, 2007. The Adaptive Significance of Sensory Bias in a Foraging Context: Floral Colour Preferences in the Bumblebee Bombus terrestris. Plos One 2.

Raine NE, Chittka L, 2008. The correlation of learning speed and natural foraging success in bumble-bees. Proceedings of the Royal Society B-Biological Sciences 275:803-808.

Raine NE, Chittka L, 2012. No Trade-Off between Learning Speed and Associative Flexibility in Bumblebees: A Reversal Learning Test with Multiple Colonies. Plos One 7.

Raine NE, Ings TC, Ramos-Rodriguez O, Chittka L, 2006. Intercolony variation in learning performance of a wild British bumblebee population (Hymenoptera : Apidae : Bombus terrestris audax). Entomologia Generalis 28:241-256.

Reznikova Z, 2008. Experimental paradigms for studying cognition and communication in ants (Hymenoptera: Formicidae). *Myrmecological News* 11:201-214.

Riddiford LM, 2012. How does juvenile hormone control insect metamorphosis and reproduction? General and Comparative Endocrinology 179:477-484.

Riechert SE, Hedrick AV, 1990. Levels of predation and genetically based antipredator behavior in the spider, Agelenopsis aperta. Animal Behaviour 40:679-687.

Riechert SE, Jones TC, 2008. Phenotypic variation in the social behaviour of the spider Anelosimus studiosus along a latitudinal gradient. Animal Behaviour 75:1893-1902.

Rittschof CC, 2017. Sequential social experiences interact to modulate aggression but not brain gene expression in the honey bee (Apis mellifera). Frontiers in Zoology 14.

Roberts G, 1996. Why individual vigilance declines as group size increases. Animal Behaviour 51:1077-1086.

Robinson GE, 1992. Regulation of division-of-labor in insect societies. Annual Review of Entomology 37:637-665.

Robinson GE, Ben-Shahar Y, 2002. Social behavior and comparative genomics: new genes or new gene regulation? Genes Brain and Behavior 1:197-203.

Robinson GE, Page RE, Huang ZY, 1994. Temporal polyethism in social insects is a developmental process. Animal Behaviour 48:467-469.

Robinson GEP, R. E., Jr., 1989. Genetic basis for division of labour in an insect society. In: The Genetics of Social Evolution. Boulder, Colorado: Westview Press.

Robson SKA, Traniello JFA, 2002. Transient division of labor and behavioral specialization in the ant Formica schaufussi. Naturwissenschaften 89:128-131.

Ross KG, Keller L, 2002. Experimental conversion of colony social organization by manipulation of worker genotype composition in fire ants (Solenopsis invicta). Behavioral Ecology and Sociobiology 51:287-295.

Rowell DM, Aviles L, 1995. Sociality in a bark-dwelling huntsman spider from australia, delena cancerides walckenaer (Araneae, sparassidae). Insectes Sociaux 42:287-302.

Rowles AD, O'Dowd DJ, 2007. Interference competition by Argentine ants displaces native ants: implications for biotic resistance to invasion. Biological Invasions 9:73-85.

Ruckstuhl KE, Neuhaus P, 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. Biological Reviews 77:77-96.

Salazar MOL, Planas-Sitja I, Sempo G, Deneubourg JL, 2018. Individual Thigmotactic Preference Affects the Fleeing Behavior of the American Cockroach (Blattodea: Blattidae). Journal of Insect Science 18.

Sasaki T, Granovskiy B, Mann RP, Sumpter DJT, Pratt SC, 2013. Ant colonies outperform individuals when a sensory discrimination task is difficult but not when it is easy. Proceedings of the National Academy of Sciences of the United States of America 110:13769-13773.

Sasaki T, Pratt SC, 2012. Groups have a larger cognitive capacity than individuals. Current Biology 22:R827-R829.

Sasaki T, Pratt SC, 2018. The Psychology of Superorganisms: Collective Decision Making by Insect Societies. Annual Review of Entomology, Vol 63 63:259-275.

Scheiner R, Barnert M, Erber J, 2003. Variation in water and sucrose responsiveness during the foraging season affects proboscis extension learning in honey bees. Apidologie 34:67-72.

Scheiner R, Erber J, Page RE, 1999. Tactile learning and the individual evaluation of the reward in honey bees (Apis mellifera L.). Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology 185:1-10.

Scheiner R, Page RE, Erber J, 2004. Sucrose responsiveness and behavioral plasticity in honey bees (Apis mellifera). Apidologie 35:133-142.

Schneider JM, Roos J, Lubin Y, Henschel JR, 2001. Dispersal of Stegodyphus dumicola (Araneae, Eresidae): They do balloon after all! Journal of Arachnology 29:114-116.

Schulz DJ, Sullivan JP, Robinson GE, 2002. Juvenile hormone and octopamine in the regulation of division of labor in honey bee colonies. Hormones and Behavior 42:222-231.

Seeley TD, 1978. Life history strategy of the honey bee, Apis mellifera. Oecologia. p. 109-118.

Seeley TD, 1982. Adaptive significance of the age polyethism schedule in honeybee colonies. Behavioral Ecology and Sociobiology 11:287-293.

Seeley TD, 1985. Honeybee ecology: Princeton University Press.

Seeley TD, 2010. Honeybee Democracy. Honeybee Democracy:1-273.

Seeley TD, Buhrman SC, 1999. Group decision making in swarms of honey bees. Behavioral Ecology and Sociobiology 45:19-31.

Seeley TD, Visscher PK, 2004. Quorum sensing during nest-site selection by honeybee swarms. Behavioral Ecology and Sociobiology 56:594-601.

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.

Seibt U, Wickler W, 1988. Interspecific tolerance in social stegodyphus spiders (Eresidae, araneae). Journal of Arachnology 16:35-39.

Seibt U, Wickler W, 1990. The Protective Function of the Compact Silk Nest of Social Stegodyphus Spiders (Araneae, Eresidae). Oecologia 82:317-321.

Settepani V, Grinsted L, Granfeldt J, Jensen JL, Bilde T, 2013. Task specialization in two social spiders, Stegodyphus sarasinorum (Eresidae) and Anelosimus eximius (Theridiidae). Journal of Evolutionary Biology 26:51-62.

Seyfarth RM, Cheney DL, Marler P, 1980. Monkey responses to 3 different alarm calls - evidence of predator classification and semantic communication. Science 210:801-803.

Sih A, Bell A, Johnson JC, 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol 19:372-378.

Sih A, Cote J, Evans M, Fogarty S, Pruitt J, 2012. Ecological implications of behavioural syndromes. Ecology Letters 15:278-289.

Sih A, Krupa J, Travers S, 1990. An experimental study on the effects of predation risk and feeding regime on the mating behavior of the water strider. American Naturalist 135:284-290.

Silk JB, 2007. The adaptive value of sociality in mammalian groups. Philosophical Transactions of the Royal Society B-Biological Sciences 362:539-559.

Simons AM, 2004. Many wrongs: the advantage of group navigation. Trends in Ecology & Evolution 19:453-455.

Sloan Wilson D, Clark AB, Coleman K, Dearstyne T, 1994. Shyness and boldness in humans and other animals. Trends in Ecology & Evolution 9:442-446.

Smith JM, 1979. Game theory and the evolution of behavior. Proceedings of the Royal Society Series B-Biological Sciences 205:475-488.

Stamps J, Groothuis TGG, 2010a. The development of animal personality: relevance, concepts and perspectives. Biological Reviews 85:301-325.

Stamps JA, Groothuis TGG, 2010b. Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differencese. Philosophical Transactions of the Royal Society B-Biological Sciences 365:4029-4041.

Stevens M, Merilaita S, 2009. Animal camouflage: current issues and new perspectives. Philosophical Transactions of the Royal Society B-Biological Sciences 364:423-427.

Strassmann J, 2001. The rarity of multiple mating by females in the social Hymenoptera. Insectes Sociaux 48:1-13.

Stroeymeyt N, Franks NR, Giurfa M, 2011. Knowledgeable individuals lead collective decisions in ants. Journal of Experimental Biology 214:3046-3054.

Sueur C, King AJ, Conradt L, Kerth G, Lusseau D, Mettke-Hofmann C, Schaffner CM, Williams L, Zinner D, Aureli F, 2011. Collective decision-making and fission-fusion dynamics: a conceptual framework. Oikos 120:1608-1617.

Sullivan J, Jassim O, Fahrbach S, Robinson G, 2000. Juvenile hormone paces behavioral development in the adult worker honey bee. Hormones and Behavior. p. 1-14.

Sumpter DJT, Pratt SC, 2009. Quorum responses and consensus decision making. Philos T R Soc B 364:743-753.

Suryanarayanan S, Hermanson JC, Jeanne RL, 2011. A Mechanical Signal Biases Caste Development in a Social Wasp. Current Biology 21:231-235.

Suryanarayanan S, Jeanne RL, 2008. Antennal Drumming, Trophallaxis, and Colony Development in the Social WaspPolistes fuscatus(Hymenoptera: Vespidae). Ethology 114:1201-1209.

Suselbeek L, Emsens W-J, Hirsch BT, Kays R, Rowcliffe JM, Zamora-Gutierrez V, Jansen PA, 2014. Food acquisition and predator avoidance in a Neotropical rodent. Anim Behav 88:41-48. Szathmary E, Smith JM, 1995. The major evolutionary transitions. Nature 374:227-232.

Tener JS, 1954. A preliminary study of the musk-oxen of Fosheim Peninsula, Ellesmere Island, NWT: Canadian Wildlife Service.

Theraulaz G, Bonabeau E, 1995. Coordination in distributed building. Science 269:686-688.

Theraulaz G, Bonabeau E, Deneubourg J-L, 1998a. The origin of nest complexity in social insects. Complexity 3:15-25.

Theraulaz G, Bonabeau E, Deneubourg JL, 1998b. Response threshold reinforcement and division of labour in insect societies. Proceedings of the Royal Society B-Biological Sciences 265:327-332.

Theraulaz G, Bonabeau E, Nicolis SC, Sole RV, Fourcassie V, Blanco S, Fournier R, Joly JL, Fernandez P, Grimal A, Dalle P, Deneubourg JL, 2002. Spatial patterns in ant colonies. Proceedings of the National Academy of Sciences of the United States of America 99:9645-9649.

Thomson RL, Tomas G, Forsman JT, Broggi J, Monkkonen M, 2010. Predator proximity as a stressor in breeding flycatchers: mass loss, stress protein induction, and elevated provisioning. Ecology 91:1832-1840.

Thornton A, Clutton-Brock T, 2011. Social learning and the development of individual and group behaviour in mammal societies. Philosophical Transactions of the Royal Society B-Biological Sciences 366:978-987.

Tibbetts EA, Huang ZY, 2010. The Challenge Hypothesis in an Insect: Juvenile Hormone Increases during Reproductive Conflict following Queen Loss in Polistes Wasps. American Naturalist 176:123-130.

Tizo-Pedroso E, Del-Claro K, 2011. Is There Division of Labor in Cooperative Pseudoscorpions? An Analysis of the Behavioral Repertoire of a Tropical Species. Ethology 117:498-507.

Toth AL, Robinson GE, 2005. Worker nutrition and division of labour in honeybees. Animal Behaviour 69:427-435.

Traniello JFA, Fujita MS, Bowen RV, 1984. Ant foraging behavior - ambient-temperature influences prey selection. Behavioral Ecology and Sociobiology 15:65-68.

Vanhonk C, Hogeweg P, 1981. The ontogeny of the social-structure in a captive bombus-terrestris colony. Behavioral Ecology and Sociobiology 9:111-119.

Visscher PK, 2007. Group decision making in nest-site selection among social insects. Annual Review of Entomology 52:255-275.

Vollrath F, 2006. Spider silk: Thousands of nano-filaments and dollops of sticky glue. Curr Biol 16:R925-R927.

Waibel M, Floreano D, Magnenat S, Keller L, 2006. Division of labour and colony efficiency in social insects: effects of interactions between genetic architecture, colony kin structure and rate of perturbations. Proc Biol Sci 273:1815-1823.

Wallraff HG, 1978. Social interrelations involved in migratory orientation of birds - possible contribution of field studies. Oikos 30:401-404.

Wang J, Wurm Y, Nipitwattanaphon M, Riba-Grognuz O, Huang YC, Shoemaker D, Keller L, 2013. A Y-like social chromosome causes alternative colony organization in fire ants. Nature 493:664-668.

Ward AJW, Herbert-Read JE, Sumpter DJT, Krause J, 2011. Fast and accurate decisions through collective vigilance in fish shoals. Proceedings of the National Academy of Sciences of the United States of America 108:2312-2315.

Ward AJW, Sumpter DJT, Couzin LD, Hart PJB, Krause J, 2008. Quorum decision-making facilitates information transfer in fish shoals. Proceedings of the National Academy of Sciences of the United States of America 105:6948-6953.

Werner EE, Peacor SD, 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083-1100.

West-Eberhard MJ, 2003. Developmental plasticity and evolution: Oxford University Press.

Wheeler DE, Buck N, Evans JD, 2006. Expression of insulin pathway genes during the period of caste determination in the honey bee, Apis mellifera. Insect Molecular Biology 15:597-602.

Whitehouse MEA, Lubin Y, 1999. Competitive foraging in the social spider Stegodyphus dumicola. Animal Behaviour 58:677-688.

Wickler W, Seibt U, 1993. Pedogenetic sociogenesis via the sibling-route and some consequences for stegodyphus spiders. Ethology 95:1-18.

Wiernasz DC, Cole BA, Cole BJ, 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.

Wilcox RS, Jackson RR, 1998. Cognitive abilities of araneophagic jumping spiders. Animal Cognition in Nature. p. 411-434.

Williams TM, Estes JA, Doak DF, Springer AM, 2004. Killer appetites: Assessing the role of predators in ecological communities. Ecology 85:3373-3384.

Wilson DS, 1975. Theory of group selection. Proceedings of the National Academy of Sciences of the United States of America 72:143-146.

Wilson DS, Sober E, 1989. Reviving the superorganism. Journal of Theoretical Biology 136:337-356.

Wilson EO, 1971. The Insect Societies. Cambridge, MA: Harvard University Press.

Wolf JB, Brodie ED, Cheverud JM, Moore AJ, Wade MJ, 1998. Evolutionary consequences of indirect genetic effects. Trends in Ecology & Evolution 13:64-69.

Wolf JB, Brodie ED, Moore AJ, 1999. Interacting phenotypes and the evolutionary process. II. Selection resulting from social interactions. American Naturalist 153:254-266.

Wolf M, van Doorn GS, Leimar O, Weissing FJ, 2007. Life-history trade-offs favour the evolution of animal personalities. Nature 447:581-584.

Wray MK, Mattila HR, Seeley TD, 2011. Collective personalities in honeybee colonies are linked to colony fitness. Animal Behaviour 81:559-568.

Wray MK, Seeley TD, 2011. Consistent personality differences in house-hunting behavior but not decision speed in swarms of honey bees (Apis mellifera). Behavioral Ecology and Sociobiology 65:2061-2070.

Wright C, Holbrook CT, Pruitt J, 2014a. Animal personality aligns task specialization and task proficiency in a spider society. Proceedings of the National Academy of Sciences.

Wright CM, Holbrook CT, Pruitt JN, 2014b. Animal personality aligns task specialization and task proficiency in a spider society. Proceedings of the National Academy of Sciences of the United States of America 111:9533-9537.

Wright CM, Hyland TD, Izzo AS, McDermott DR, Tibbetts EA, Pruitt JN, 2017a. Polistes metricus queens exhibit personality variation and behavioral syndromes. Current Zoology.

Wright CM, Keiser CN, Pruitt JN, 2015. Personality and morphology shape task participation, collective foraging and escape behaviour in the social spider Stegodyphus dumicola. Animal Behaviour 105:47-54.

Wright CM, Keiser CN, Pruitt JN, 2016a. Colony personality composition alters colony-level plasticity and magnitude of defensive behaviour in a social spider. Animal Behaviour. p. 175-183.

Wright CM, Lichtenstein JLL, Montgomery GA, Luscuskie LP, Pinter-Wollman N, Pruitt JN, 2017b. Exposure to predators reduces collective foraging aggressiveness and eliminates its relationship with colony personality composition. Behavioral Ecology and Sociobiology 71:126.

Wright CM, Skinker VE, Izzo AS, Tibbetts EA, Pruitt JN, 2016b. Queen personality type predicts nest-guarding behaviour, colony size and the subsequent collective aggressiveness of the colony. Animal Behaviour.

Yip EC, 2014. Ants versus spiders: interference competition between two social predators. Insectes Sociaux 61:403-406.

Yip EC, Powers KS, Aviles L, 2008. Cooperative capture of large prey solves scaling challenge faced by spider societies. Proceedings of the National Academy of Sciences of the United States of America 105:11818-11822.

Yip EC, Rayor LS, 2011. Do social spiders cooperate in predator defense and foraging without a web? Behavioral Ecology and Sociobiology 65:1935-1947.

Yip EC, Rayor LS, 2013. The influence of siblings on body condition in a social spider: is prey sharing cooperation or competition? Animal Behaviour 85:1161-1168.

Zayed A, Robinson GE, 2012. Understanding the Relationship Between Brain Gene Expression and Social Behavior: Lessons from the Honey Bee. Annual Review of Genetics, Vol 46 46:591-615.

Zhang SW, Lehrer M, Srinivasan MV, 1999. Honeybee memory: Navigation by associative grouping and recall of visual stimuli. Neurobiology of Learning and Memory 72:180-201.