



Original Article

Collective responses to heterospecifics emerge from individual differences in aggression

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Variation in individual behavior among group members impacts collective outcomes. The ability of both individuals and groups to out-compete others can determine access to resources. The invasive Argentine ant, *Linepithema humile*, dominates resources and displaces native species. To determine how access to resources by groups of *L. humile* is impacted by their behavioral composition, we first determined that *L. humile* workers consistently vary in aggressive behavior. We then asked if variation in aggression within a group influences the group's ability to access a resource in the presence of cues of a native species, *Tapinoma sessile*. We found that the behavioral composition of *L. humile* groups impacted the groups' collective response to cues of *T. sessile*. Group behavior was the result of mostly additive, rather than synergistic, combinations of the behaviors of the group members. The behavior of groups that contained 50% highly aggressive and 50% low-aggression individuals was similar to the average of the behaviors of groups of all highly aggressive and groups of all low-aggression individuals. Uncovering the mechanisms that allow social invasive species to dominate the ecological communities they invade can inform the mitigation of invasion.

Key words: Argentine ants, collective behavior, group composition, invasive species, personality.

INTRODUCTION

Collective behavior emerges from individual-based, local rules (Sumpter 2010). Traditionally, groups have been viewed as aggregates of identical individuals (Couzin et al. 2002). However, individuals vary in their behavior (Sih et al. 2004; Reale et al. 2007), such as aggression (van Oers et al. 2005), exploration (Fraser et al. 2001), and boldness (Ariyomo and Watt 2012). In social insects, workers differ in the types of tasks they perform (Jandt et al. 2014; Jaisson et al. 1988; Gordon 1996) and in how effectively they perform those tasks (Pinter-Wollman et al. 2012). This variation in individual behavior results in heterogeneous group compositions and such behavioral variation in social groups impacts collective outcomes (Pinter-Wollman 2012; Jandt et al. 2014; Modlmeier et al. 2014). Group behavior can reflect the exact composition of the group, for example, the mean behavior of its constituents, which we refer to as additive effects. Alternatively, group behavior can exceed the simple addition of its constituents' behaviors, referred to as synergistic effects. Such synergies often arise from group members influencing the behavior of each other through social interactions (Robson and Traniello 1999; Pinter-Wollman 2012; Modlmeier et al. 2014).

Variation in the aggressive behavior of individuals in a group can determine the success of the group as a whole. For example, the composition of aggressive individuals in wolf packs determines which pack will win in intraspecific encounters (Cassidy et al. 2015). Furthermore, the number of aggressive individuals in a group is positively related with successfully competing with conspecifics (Lichtenstein et al. 2016) and obtaining prey, which can impact the fitness of group members (Pruitt and Goodnight 2014). The behavioral composition of a group may impact its success when faced with heterospecifics. Trait variation can determine interspecific competition, which shapes the structure of ecological communities (Bolnick et al. 2011) and variation in behavior may contribute to the ability of species to disperse and invade new ranges (Duckworth 2008; Cote et al. 2010; Fogarty et al. 2011; Wolf and Weissing 2012). Here, we examine how variation in aggressive behavior within groups of an invasive social species affects the groups' response to heterospecifics.

Invasive species often outcompete native species by dominating food sources and rapidly recruiting individuals to new resources (Davidson 1998; Holway 1999; Rowles and O'Dowd 2007). The Argentine ant, *Linepithema humile*, is a dominant, successful invasive species (Suarez et al. 2001) with low intraspecific aggression in its introduced range (Holway et al. 1998; Suarez et al. 2002). *Linepithema humile* have become established in their invaded range, and have been expanding their reach by rapidly acquiring resources

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(Human and Gordon 1996); recruiting in greater numbers than native species to resources (Holway 1998, 1999); and changing the structure of the ecological community (Sanders et al. 2003).

Linepithema humile often rely on group-level processes to successfully displace native species (Human and Gordon 1996, 1999; Holway 1999; Buczkowski and Bennett 2008). Workers vary in their aggressive behavior based on past experiences with non-nest-mates (Van Wilgenburg et al. 2010) and colonies vary in the level of aggression of their workers (Blight et al. 2017). The odorous house ant, *Tapinoma sessile*, is native to California and is impacted by the presence of *L. humile* because the two species occupy a similar ecological niche (Ward 1987; Human and Gordon 1999). Although *L. humile* often lose in one-on-one interactions with native species, such as *T. sessile* (Holway 1999; Rowles and O'Dowd 2007; Buczkowski and Bennett 2008), *L. humile* have succeeded in displacing *T. sessile* from their native range, in part due to *L. humile*'s large colony size (Holway 1999; Holway and Case 2000), and cooperative fighting (Buczkowski and Bennett 2008). Chemicals play an important role in the interactions between *L. humile* and native ants (Sorrells et al. 2011), and both *L. humile* and *T. sessile* have been observed releasing chemicals when fighting or when in close contact to one another (Buczkowski and Bennett 2008). Thus, it is possible that chemicals laid in the environment could be used by *L. humile* as cues for the presence of native species.

To uncover the role of group composition in the domination of *L. humile* over native species, we examined the responses of *L. humile* to cues of *T. sessile*. We first established that aggressive behavior varies among individuals in a consistent way. To then determine if the group response of *L. humile* to *T. sessile* cues results from the combination, either additive or synergistic, of the aggression of the individuals comprising the group, we compared the collective behaviors of groups with three compositions: 1) all highly aggressive individuals, 2) all low-aggression individuals, and 3) groups in which half the individuals were highly aggressive and the other half exhibited low aggression (mixed groups). We then examined the behavior of individually marked workers in mixed groups to determine which individuals responded to the *T. sessile* cues. If group response emerges from additive effects, we would expect the mixed groups to behave similarly to the average behaviors of the other two uniform groups. We would further expect the highly aggressive individuals in the mixed groups to behave like the individuals in the groups comprised of only highly aggressive individuals and the low-aggression individuals in the mixed group to behave like their counterparts in the uniform low-aggression groups. Alternatively, if group behavior emerges from synergistic effects, we expect the behavior of the mixed groups to be similar to one of the two uniform groups and the behavior of the individuals comprising the mixed groups to be different from their behavior observed when they are not in a group.

METHODS

Collection and maintenance of animals

We collected approximately 800 *L. humile* workers from foraging trails of one functional colony at the UCLA Botanical Gardens, where *L. humile* are the only ant species we observed, in January 2017. Ants were housed in a 5200 mL plastic box coated with fluon to prevent escape. Ants were provided with a nest, sugar water, and water ad libitum. To determine the response of *L. humile* to a native species, we collected approximately 800 foragers of *T. sessile* from foraging trails of one colony in a residential area in Venice,

Los Angeles, where no *L. humile* are found and *T. sessile* is the predominant ant species (Noa Pinter-Wollman, personal observations). *Tapinoma sessile* ants were kept in the lab in a separate container from the *L. humile* workers and under the same conditions.

Individual aggression

To determine the aggressive behavior of *L. humile* workers, we examined their response to workers of *T. sessile*. We placed an *L. humile* worker in a 60 mL plastic cup, coated with fluon, for 5 min to acclimate. We then added a tethered *T. sessile* worker to the cup and observed the response of the *L. humile* worker for 5 min continuously. Individuals were selected haphazardly for these assays. We used tethered *T. sessile* (Figure 1A) to minimize the response they might have to attacks by *L. humile*, such as escaping. Tethering was conducted by looping one end of a string around the thorax of a *T. sessile* worker and tying the other end to a holdfast above the ant, thus preventing her from escaping. Tethered *T. sessile* workers were never observed fighting back.

To quantify the aggressive behavior of *L. humile*, we recorded the behaviors described in Table 1 that were exhibited during the 5-min continuous observation, based on Buczkowski and Bennett (2008) and Suarez et al. (2002). Each behavior was assigned a weight (Table 1), based on how aggressive it was considered (Buczkowski and Bennett 2008). These weights were used to calculate the aggression score of each individual as the sum of the weighted scores (Table 1) of the observed behaviors when determining the distribution of aggression in the population ($n = 72$ ants) and when examining the repeatability of aggressive behavior ($n = 18$ ants). To determine if aggressive behavior is repeatable, we tested the aggression of 18 ants over 4 consecutive days (once on each day). Subsequently, behaviors were assigned to a category from 1 to 4 where 1 was assigned to the least aggressive behaviors, and 4 to the most aggressive behaviors (Table 1) following Buczkowski and Bennett (2008) and Suarez et al. (2002). Based on the observed distribution of aggressive behavior (detailed in the results) when screening individuals for the group composition experiment (detailed below), we considered workers that exhibited at least one of the most extreme aggressive behaviors (category 3 or 4) to be highly aggressive. Workers that did not exhibit any of these extremely aggressive behaviors were considered to be low-aggression individuals.

We further determined the relationship between aggressive behavior and spatial exploration, a repeatable behavior in *L. humile*

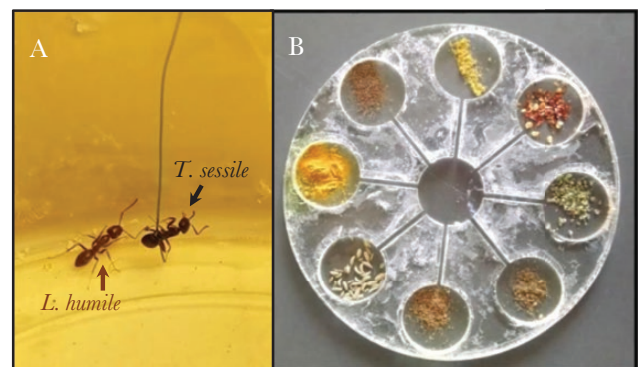


Figure 1

Behavioral methods. (A) *Linepithema humile* worker attacking a tethered *T. sessile* worker. (B) Eight-armed maze with spices used to test the spatial exploration of individual *L. humile* workers.

Table 1
Ethogram of *L. humile* aggressive behaviors in the presence of a tethered *T. sessile* worker

Behavior	Description of behavior	Category	Weighted score
Antennation	Contacting or feeling with antennae	1	0.5
Approach	Walking up to opponent	1	1.5
Prolonged contact	Close contact for extended period of time (>10 s); not fighting	1	1.5
Opening of mandibles	Spreading open mandibles towards opponent	2	2
Mounting	Climbing on top of opponent	2	2
Gaster tilt	Lifting gaster	2	2
Mandible lock	Using mandibles to grab opponent's mandibles	3	3
Biting	Biting into opponent	3	3.5
Fighting	Engaging in a fight with opponent, including close contact/attacks on opponent	4	4
Limb/body part detachment	Pulling off the limbs or body parts of opponent	4	5
Prolonged fighting	Fighting for extended period of time (>60 s)	4	5
Killing	Killing opponent during a fight	4	6

workers (Page et al. 2019). We examined the relationship between aggression and spatial exploration because the collective behaviors we observed (detailed below) could be interpreted as either a result of variation in aggression or variation in spatial exploration. To examine the relationship between aggression and spatial exploration, we tested another 54 *L. humile* workers in both the aggression assay described above (using continuous scoring) and an established exploration assay described in Hui and Pinter-Wollman (2014) and Modlmeier and Foitzik (2011). In short, spatial exploration was quantified as the number of visits (including repeated visits) a worker made during 5 min to the arms of an 8-armed maze in which each arm had a unique spice (Figure 1B). For a list of spices used see Hui and Pinter-Wollman (2014). It has been recently shown that this assay provides a reliable, repeatable, and real-time quantification of the spatial exploration of *L. humile* workers in an open field and in natural conditions (Page et al. 2019).

Effect of group composition on collective behavior

To determine the effect of behavioral composition on group collective behavior, we assembled three types of groups, each containing 10 workers: 1) highly aggressive, 2) mixed (half highly aggressive and half low-aggression individuals), and 3) all low-aggression individuals. Although *L. humile* colonies are large, we used groups of 10 individuals because this is a feasible size for a propagule (Hee et al. 2000) — the social unit that disperses and establishes in new territory. We replicated the experiment 8 times with each group type. To determine the collective response of groups to cues of *T. sessile*, we placed each experimental group in a plastic arena 12 × 18 cm with walls coated with fluon to prevent the escape of ants. Initially, the group was contained in a 32 mL vial plugged with a cotton ball. We considered this vial as the ants' "nest." After 6 h in the nest, we began the assay to quantify collective behavior by removing the cotton ball plug and allowing the ants to move freely in the arena. The nest vial was placed on one side of the arena and sugar water and tuna were placed on the opposite side. Between the nest and food, we placed a 12 × 0.75 cm strip of filter paper that had been placed in a box with approximately 100 *T. sessile* workers for a week prior to the experiment. Ants could not reach the food without crossing the strip (Supplementary Figure S1). During the week, the strip was in the container of the *T. sessile* workers it absorbed their strong scent, which could be smelled even by the human experimenter, and so was most likely apparent to the *L. humile* workers. Studies of ant competition show that workers leave chemical footprints where

they walk, after only 5–60 min, and that other species respond to these cues (Wust and Menzel 2017). The behavior of the ants in the arena was videotaped for further analysis for 15 min using a Canon Vixia HFR50 camcorder. To quantify the group-level response, we used the image analysis software AnTracks (<http://antracks.martinstumpe.com/>) to quantify the following: 1) number of times *L. humile* workers arriving from the nest climbed onto the strip with *T. sessile* cues, 2) number of times *L. humile* workers continued from the strip to the food, and 3) total time spent by all ants on the strip (Supplementary Figure S1). Such interactions with the strip with *T. sessile* cues would suggest that the *L. humile* workers are not deterred by cues of native species and can thus invade new sites in which native species are present. These measures were obtained from the automated image analysis software which was "blind" to the group type, thus avoiding observer bias.

To further determine the role of highly aggressive and low-aggression workers in the mixed group, we repeated this collective assay on 8 more mixed groups in which highly aggressive workers were painted one color and low-aggression workers were painted a different color, using acrylic paint. In these experiments, we recorded which of the ants, highly aggressive or low-aggressive individuals, interacted with the filter paper strip for all interactions with the paper strip.

Data analysis

The repeatability of aggression over 4 days was quantified using an Intraclass Correlation Coefficient (ICC) (Bell et al. 2009). The relationship between aggression and spatial exploration was tested using a Pearson's Correlation. To compare the collective behavior of the three group types, we conducted nonparametric Kruskal–Wallis tests followed by post-hoc Dunn's tests — one for each of the three variables obtained using image analysis (number of strip-crossings from the nest, to the food, and time on the strip).

To determine if the observed behavior of the mixed group was the result of additive or synergistic effects of the group members' behavior, we compared the observed behavior of mixed groups with the mean behavior of all highly-aggressive and all low-aggression groups using an exact permutation test. If the observed behavior of the mixed groups was similar to the average behavior of the two other group types, that would support the hypothesis that the behavior of the mixed group was a result of simple additive effects, alternatively, a significant difference would suggest synergistic effects (Hui and Pinter-Wollman 2014). For each of the three measures of interactions with the cues of *T. sessile* (number of

strip-crossing from the nest, to the food, and time on the strip), we computed all 64 (8×8) possible mean values of the 8 all highly-aggressive groups and the 8 all low-aggression groups. We then examined the percentile in which each of the 8 experimental mixed group results fell within this estimated distribution of 64 means to estimate the probability that each of the observed 8 mixed group results would be predicted by a simple additive rule. We averaged the 8 percentiles to estimate the P -value for whether the mixed groups significantly deviated from the mean of the behavior of the all highly-aggressive and all low-aggression groups. A small P -value (<0.05) would lead us to reject the additive hypothesis (for a similar computation, see Hui and Pinter-Wollman (2014)).

To compare the behavior of highly aggressive and low-aggression ants in the mixed groups, in which we painted ants according to their aggression, we compared number of strip-crossings from the nest, to the food, and amount of time on the strip, per ant. To obtain per-ant values, we divided each measure by the number of ants of a certain aggression type in a group ($n = 5$ of each type in the mixed groups and $n = 10$ for the homogenous groups). This computation allowed us to compare among the three types of groups that contained different numbers of highly aggressive and low-aggression workers.

RESULTS

Aggressive behavior varied consistently among workers and did not relate to their spatial exploration. Aggression score of workers ranged from 0 to 46 and deviated from a unimodal distribution (Hartigan's Dip Test [Hartigan and Hartigan 1985], $P=0.04$ implemented in the R package "dipTest") and exhibited a bimodal distribution (bimodality coefficient = 0.65, which is greater than the threshold of 0.55 that describes a unimodal distribution (Pfister et al. 2013)). Further, individuals that never exhibited behaviors in categories 3 or 4 (Table 1) all fell within a unimodal distribution with an average aggression of 4.82 and individuals that exhibited at least one behavior in category 3 or 4 produced a distinct unimodal distribution with a mean of 26.33 (Figure 2A). We therefore

used category 3 or 4 as a proxy for identifying highly aggressive individuals when selecting individuals for the group trials. When aggression was tested repeatedly over 4 days, workers exhibited extremely high persistence, ICC = 0.86 (confidence interval [CI]: 0.74, 0.94; Figure 2B). Furthermore, aggressive behavior was not related to spatial exploration. We did not detect a significant relationship between aggression score and the number of visits an ant made to the arms in the 8-armed maze in the 54 individuals that we tested (Pearson's correlation: $r = 0.13$, $P = 0.336$).

Group composition had a significant effect on the propensity of workers to interact with the *T. sessile* cues. Groups significantly differed in how many times they crossed from the nest to the strip (Kruskal–Wallis: $\chi^2 = 14.8$, $df = 2$, $P < 0.001$; Figure 3A) and from the strip to the food (Kruskal–Wallis: $\chi^2 = 14.29$, $df = 2$, $P < 0.001$; Figure 3B). On average, groups of all highly aggressive individuals engaged in 475% more crossings from the nest and 336% more to the food compared with the groups comprised of all low-aggression individuals. Furthermore, the time individuals spent on the strip significantly differed among groups (Kruskal–Wallis: $\chi^2 = 16.22$, $df = 2$, $P < 0.0001$; Figure 4). On average, groups of all highly aggressive individuals spent 836% more time on the strip compared with the groups comprised of all low-aggression individuals and 47% more time compared with the mixed groups.

Comparing the observed results from the mixed group with all possible mean values of the all highly aggressive and the all low-aggression groups supported the additive hypothesis. The observed values of crossing the strip from the nest in the mixed groups did not differ from the expected mean (exact permutation test: $P = 0.391$), and neither did the number of crossings to the food (exact permutation test: $P = 0.71$), or the time ants spent on the strip (exact permutation test: $P = 0.5$).

In the mixed groups in which workers were painted according to their behavior, the propensity to interact with the *T. sessile* cues differed between workers of different aggression, further supporting the additive hypothesis. Highly aggressive workers crossed the strip more frequently than the low-aggression individuals in the group from the nest (Kruskal–Wallis: $\chi^2 = 25.1$, $df = 3$, $P < 0.0001$; Figure 5A) and to

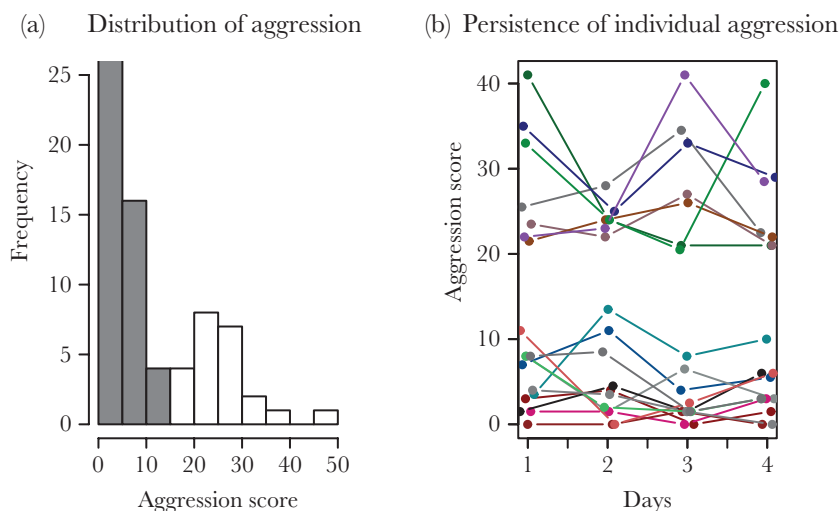
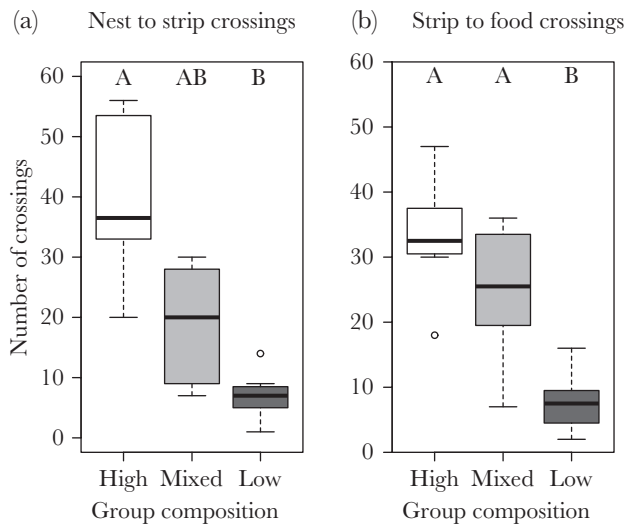


Figure 2

Individual variation in aggression. (A) Distribution of aggressive behavior of individual *L. humile* workers ($n = 72$). Workers that never exhibited a behavior in category 3 or 4 are in grey and workers that exhibited at least one behavior in category 3 or 4 are in white. (B) Aggression scores of 18 individual workers tested repeatedly over 4 days. Each color represents a single individual. Points are slightly jittered along the x axis to improve visibility.

**Figure 3**

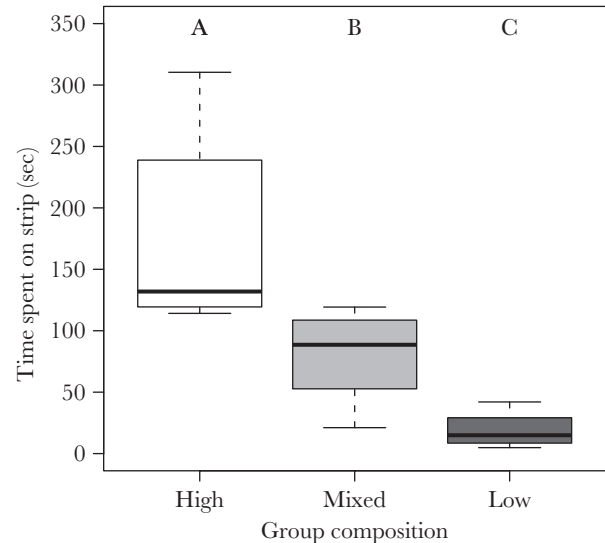
Total number of crossings from the (A) nest to strip with *T. sessile* cues and (B) strip to food of the three group types (all highly aggressive (High), mixed, and all low-aggression groups (Low), $N = 8$ of each group type). Here, and in all following figures, boxes indicate the lower and upper quartiles; horizontal lines within boxes indicate the median; whiskers extend to the 1.5 interquartile range from the box; open circles indicate outliers; and different letters indicate statistically significant differences using a post-hoc Dunn's test ($P < 0.05$).

the food (Kruskal–Wallis: $\chi^2 = 24.08$, $df = 3$, $P < 0.0001$; Figure 5B) and they spent more time on the strip (Kruskal–Wallis: $\chi^2 = 22.84$, $df = 3$, $P < 0.0001$; Figure 5C). Interestingly, the behavior of the highly aggressive individuals in the paint-marked mixed groups was similar to the behavior of the highly aggressive individuals in the all highly aggressive groups, and likewise the behavior of the low-aggression individuals in the paint-marked mixed groups was similar to the behavior of individuals in the all low-aggression groups (Figure 5).

DISCUSSION

We found that the collective responses of ants to cues from a competing species are a result of the mean behavior of individuals in the group. First, we established that there is consistent variation among individual ants in aggressive behavior (Figure 2), and that this aggressive behavior does not correlate with spatial exploration. Furthermore, we found that mixed groups, of half highly aggressive and half low-aggression *L. humile* individuals, responded to a strip of filter paper with interspecific cues of the native species, *T. sessile*, differently than groups of all highly aggressive or all low-aggression individuals (Figures 3 and 4) but not differently from the expected mean behavior of the two homogeneous groups. Furthermore, highly aggressive individuals in paint-marked mixed groups behaved similarly to highly aggressive individuals in all highly aggressive groups and low-aggression individuals in paint-marked mixed groups did not differ significantly in their behavior from the behavior of individuals in all low-aggression groups (Figure 5). These findings suggest that the collective response of a group of *L. humile* to cues of native ants is the result of an additive, rather than a synergistic joining of the group members' aggressive behavior.

The additive effects of aggression in *L. humile* at the group level might impact their ability to compete with native species. *Linepithema humile* often displace native species through aggressive

**Figure 4**

Total time, in seconds, that ants spent on the filter paper strip with *T. sessile* cues during the 15-min observation, by group composition ($N = 8$ of each group type).

encounters (Rowles and O'Dowd 2007), and success of establishment at a new location increases with group size (Hee et al. 2000). Our results suggest that as the number of highly aggressive individuals increases, the frequency of aggressive encounters between *L. humile* and native species is likely to increase. We thus expect that studies examining the aggressive behavior of *L. humile* workers at their invasion front, where they encounter native species, will find more aggressive individuals at those places compared to where *L. humile* are already established.

Aggressive behavior may have costs associated with it, such as increased risk of dying (Wolf and Weissing 2012). Thus, there may be a tradeoff at the level of the colony between maintaining highly aggressive individuals, which may help expand the colony's range through encounters with native species, but may also die during a fight, leading to a loss of the resources that the colony invested in producing these workers. In other ant species, aggressive individuals are used to defend nest sites (Knapen and Wehner 2003). Thus, if in *L. humile* highly aggressive individuals protect their nest, sending many aggressive individuals away from the nest might compromise the colony's defense, especially because *L. humile* often rely on numerical advantage to successfully outcompete other ants (Holway 1999; Buczkowski and Bennett 2008). Further work examining colonies with brood and queens to test the allocation of aggressive individuals to new territory with native species versus maintaining aggressive individuals near the nest, for protection, will shed light on how this tradeoff is managed at the collective level.

Although our results suggest mostly additive effects of individual aggression on collective behavior, some low-aggression individuals may have been influenced by the highly aggressive individuals in the mixed groups. Low-aggression individuals in mixed groups were significantly more likely to cross the strip with *T. sessile* cues towards the food, than the low-aggression individuals in the all low-aggression groups (Figure 5B) and the number of crossings from the strip to the food was not significantly different between the mixed and all highly aggressive groups (Figure 3B). It is possible that the low-aggression individuals in the mixed groups followed a pheromone trail (or some other cue)

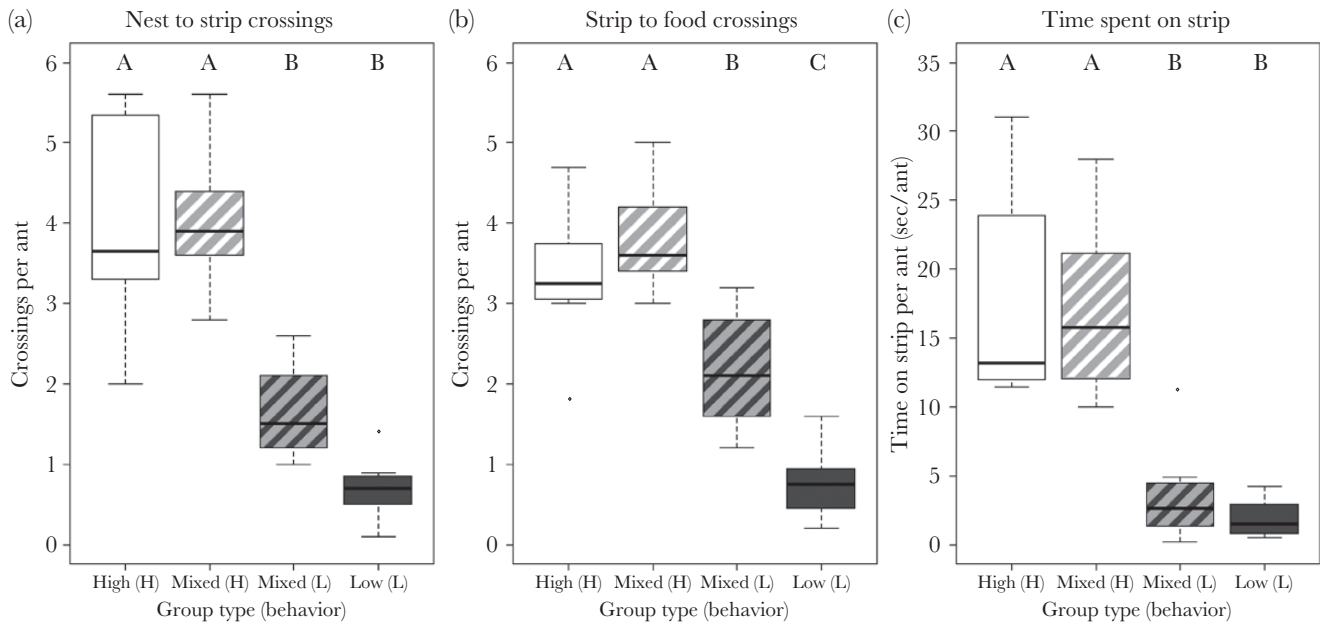


Figure 5

Number of crossings per ant from (A) nest to strip, (B) strip to food, and (C) time spent on strip. Per-ant values for individuals in the all highly aggressive groups (High), white boxes; the highly aggressive individuals (H) in the paint-marked mixed groups (Mixed), grey boxed with white hatching; the low-aggression individuals (L) in the paint-marked mixed groups (Mixed), grey boxes with black hatching; and individuals in the all low-aggression groups (Low), black boxes.

left by the aggressive individuals that crossed the strip before them (Reid et al. 2012). Further investigation of the order of arrival of individuals at the food or of trail-laying behavior in these assays would illuminate the mechanisms underlying these potential effects of highly aggressive individuals on low-aggression ones. The behavioral influence of certain individuals in a group on the behavior of others has been studied in other social systems (Modlmeier et al. 2014). In other ant species, recruitment to food begins only if there are more than a certain number of ants in the colony (Beekman et al. 2001). Perhaps in *L. humile* too, the influence of some individuals over the behavior of others is contingent on a critical number of ants.

Our result that aggression is persistent across days suggests that aggression is not plastic enough at a short time-scale to be influenced by social interactions (Pinter-Wollman et al. 2016). We found that aggressive behavior is persistent over at least 4 days. The repeatability we observed (ICC = 0.86) is comparable to some of the highest repeatabilities observed in animal behavior (Bell et al. 2009), suggesting that aggressive behavior in *L. humile* is controlled by slow-acting processes. For example, there could be developmental constraints that cause certain individuals to become more aggressive than their nestmates, such as the food they received as larvae or that they ate as adults, the temperature they developed in, or their prior social experience, which has been shown to influence aggression in *L. humile* (Van Wilgenburg et al. 2010).

Different behaviors are often correlated with each other to form a behavioral syndrome (Sih et al. 2004). For example, bold individuals are often also exploratory (Pinter-Wollman 2009). Such correlated traits may result in carry-overs between situations, which can be detrimental (Chang and Sih 2013). *Linepithema humile* workers vary in their spatial exploration which, like aggression, also has additive effects at the group level (Hui and Pinter-Wollman 2014). Although in our work individuals explored their

environment during the group trials, we did not detect a correlation between aggressive behavior and spatial exploration at the level of the individual. Thus, our group-level findings are unlikely to be a result of the exploratory tendencies of individuals. This lack of relationship between spatial exploration and aggression may benefit the colony as a whole in different situations. For example, highly aggressive, low-exploratory workers might defend nest entrances or queens (Knaden and Wehner 2003); workers that are highly aggressive and highly exploratory can increase foraging success (Pasquier and Gruter 2016) if they enable foraging in dangerous areas where there are both resources and competing ants; low-aggressive highly exploratory foragers may search for resources in regions with no competitors, potentially reducing the loss of workers to “unnecessary aggression.” Some ant species display risk-prone or risk-averse behavioral syndromes at the colony level (Bengston and Dornhaus 2014). It is possible that *L. humile* colonies exhibit a similar variety of behavioral syndromes at the colony level (Blight et al. 2017) which emerges from the colony’s behavioral composition (Pinter-Wollman 2012). For example, colonies at the invasion front might be risk-prone (with more highly aggressive, exploratory workers) and colonies at the initial site of invasion might be risk-averse (with more low-aggressive, low-exploratory workers).

In conclusion, our work highlights that the aggressive behavior of *L. humile* workers can be added to predict the collective response of a colony to native species. Thus, in some systems, the effects of individual phenotypes on collective behavior may be additive rather than synergistic. Uncovering why in some systems and situations we observe additive effects and in others we find synergistic effects is an open question. Perhaps the size of the collective unit and the mechanisms by which the collective behavior is coordinated determine the way in which collective behavior emerges from the actions of individuals.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Neumann and Pinter-Wollman (2019).

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