

Species-specific influence of group composition on collective behaviors in ants

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Abstract The success of a social group is often driven by its collective characteristics and the traits of its individuals. Thus, understanding how collective behavior is influenced by the behavioral composition of group members is an important first step to understand the ecology of collective personalities. Here, we investigated how the efficiency of several group behaviors is influenced by the aggressiveness of its members in two species of *Temnothorax* ants. In our manipulation of group composition, we created two experimentally reconstituted groups in a split-colony design, i.e., each colony was split into an aggressive and a docile group of equal sizes. We found strong species-specific differences in how collective behaviors were influenced by its group members. In *Temnothorax longispinosus*, having more aggressive individuals improved colony defense and nest relocation efficiency. In addition, source colony identity strongly influenced group behavior in *T. longispinosus*, highlighting that manipulations of group compositions must control for the origin of the chosen individuals. In contrast, group composition and source colony did not influence collective behaviors in *Temnothorax curvispinosus*. This suggests that the mechanisms regulating collective behaviors via individual differences in behavior might differ among even closely related species.

Keywords Collective behavior · Group composition · Personality · Aggression · Nest relocation · Manipulation · Social insects

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Introduction

The rise and fall of societies is often driven by their collective properties and the individual traits of its members (Wilson 1987; Pruitt 2013). Thus, studying how group characteristics are formed by the traits of its members is an important first step to understand the ecology of collective behaviors. So far, few studies have empirically examined how the personalities of individuals affect group behavior (but see Kurvers et al. 2011). This is surprising, given the rich literature on collective behavior, group performance, and decision making pertaining to both animal and human societies (e.g., ants: Pratt et al. 2002; Gordon et al. 2011; fish: Sumpter et al. 2008; Ward et al. 2008; birds: Liker and Bókonyi 2009; humans: Kerr and Tindale 2004). Furthermore, researchers have long recognized that group dynamics can be influenced by a few highly influential “keystone individuals” (Modlmeier et al. 2014).

During the last decade, an increasing number of studies have investigated the fitness consequences of animal personalities, i.e., consistent individual variation in behavior across time and/or contexts within animal species (Dall et al. 2004; Smith and Blumstein 2008; Sih et al. 2012). However, more recent studies have extended the concept of animal personalities to the group level and have revealed that collective personalities, whereby groups differ consistently in their collective behavior, can also be a major driver of individual fitness and group success. For instance, honeybee colonies with a more aggressive colony defense have an increased growth and winter survival rate (Wray et al. 2011). Or, in acorn ants, productivity (per capita offspring production) is higher in colonies that are better at reconstructing their nest after disturbance (Scharf et al. 2012). Further, docile social spider colonies are able to grow faster than their more aggressive counterparts but suffer in return from a higher extinction rate (Pruitt 2013). Despite this surge of interest in the interplay of between-individual variation and collective (aka “colony-

level”) animal personalities, empirical studies linking personalities on the individual and group levels are still scarce, as pointed out for social insect societies by several authors (Pinter-Wollman 2012; Jeanson and Weidenmüller 2013; Jandt et al. 2014).

Behavioral variation within groups is thought to be an integral part of division of labor, i.e., the specialization of individuals on distinct tasks, which is assumed to be a major component for the ecological success of social insects (Oster and Wilson 1978; Wilson 1987; Beshers and Fewell 2001). Also, consistent with this prediction, comparative studies on different subsocial and social spider species have shown that the evolution of sociality is accompanied with an increase in adaptive behavioral variation (Pruitt et al. 2012). Theoretical studies suggest that a diverse group composition, i.e., higher within-group variation in behavior, should increase group performance: mathematical models have shown that social heterosis can explain the maintenance of within-group variation through mutualistic benefits of diverse group members (Nonacs and Kapheim 2007; Nonacs and Kapheim 2008). Recent studies on social spiders (Pruitt and Riechert 2011b) and acorn ants (Modlmeier and Foitzik 2011) support these models, demonstrating that higher within-group variation in aggressive behavior is positively associated with group productivity. In bumblebees, however, mean behavioral phenotype and reduced variation in morphology, i.e., body size, were stronger predictors of colony performance than increased behavioral variation (Jandt and Dornhaus 2014). Consequently, mean behavioral phenotype could sometimes be equally or, as the previous example showed, even *more* important than within-group behavioral variation.

To what extent collective performance benefits from behavioral diversity presumably depends on the behaviors studied. Moreover, in some cases, behaviorally diverse groups might be generalists in terms of performing various collective behaviors well but show inferior performance compared to specialists for a particular behavior (cf. “Jack-of-all-trades, master-of-none”). Consequently, we reason that every collective behavior might have an optimal mean behavioral phenotype and distribution of behavioral types (Oster and Wilson 1978; Sih and Watters 2005; Dyer et al. 2009; Hui and Pinter-Wollman 2014) and that the profitability of within-group variation could differ dramatically across systems. For instance, productivity in acorn ants in the laboratory was highest in colonies with a lower mean brood care behavior and a more right skewed distribution of brood carers (Modlmeier et al. 2012).

Pinter-Wollman (2012) suggested that between-group differences in collective behavior can arise via three mechanisms: (H1) groups differ in the average behavior of their members, (H2) groups contain different behavioral

distributions, or (H3) variation in the local environment. The first two hypotheses were supported by a recent study on social spiders of the species *Stegodyphus sarasinorum* showing that collective prey capture was best described by the average and most extreme (boldest) group members (Pruitt et al. 2013). Similarly, group exploratory behavior in feral guppy shoals (*Poecilia reticulata*) was linked to the behavior of the least exploratory and the most social individuals in the group (Brown and Irving 2014). In the ant *Rhytidoponera confusa*, the number of highly aggressive workers per colony was positively correlated with various colony defense measures, indicating that inter-group differences in colony defense might be partially due to different group compositions (Crosland 1990). The third hypothesis was supported by a study on harvester ants (*Messor andrei*) demonstrating that weather and nest structure can influence foraging activity and response to disturbance (Pinter-Wollman et al. 2012). Consequently, we argue that subtle differences in group composition are likely to be an integral part of collective personalities and group success.

In this study, we investigate Pinter-Wollman’s first two hypotheses: how does mean (H1) and distribution (H2) of individual worker aggressiveness influence collective behavior in acorn ants of the species *Temnothorax longispinosus* and *Temnothorax curvispinosus*. To address these hypotheses, we use a split-colony design where we manipulate the distribution of aggressive and docile workers by splitting each colony into an aggressive and a docile group. Both ant species inhabit preformed cavities in acorns, hickory nuts, or twigs. They are common in deciduous forests across the eastern USA and well-suited for this experiment, because the artificial group size of 20 workers resembles natural-occurring variation in the number of workers per nest (Headley 1943). Further, colonies can split into multiple polydomous subunits so that our split-colony design resembles a common natural-occurring phenomenon, the important difference being that we finely manipulated group composition.

We reason that group composition will have major adaptive value for colonies because recent studies on *T. longispinosus* ants have linked within-group variation in worker personalities to colony productivity (Modlmeier and Foitzik 2011; Modlmeier et al. 2012). Newly established aggressive and docile groups (each contained 20 workers) were experimentally established in the laboratory and then confronted with a series of collective tasks in order to compare the efficiency of their collective behaviors. We examined the following collective behaviors: colony defense, nest relocation, brood recovery, and nest reconstruction. Colony-level defense is favored in *T. longispinosus* when slavemaking ants (social parasites that steal brood) are present, as it allows workers to rescue more brood when they get invaded by a slavemaking queen (Pamminger et al. 2012). We expect that colony-level defense might be slightly less important in *T. curvispinosus*, because

the co-evolutionary arms race between *T. curvispinosus* and *slavemaking ants* in Ohio is less advanced (Brandt and Foitzik 2004). Fast and efficient nest relocation and brood recovery are presumed to be ecologically important behaviors in acorn ants: colonies are forced to relocate their nest several times a year, because their nest sites (acorns, hickory nuts, and twigs) decompose during the warm summer months and become limited at the end of the year (Foitzik and Heinze 1998). Lastly, nest reconstruction (see Franks and Deneubourg 1997) is not only highly repeatable but also positively related to productivity in the European *Temnothorax nylander* (Scharf et al. 2012).

We predict that if worker personalities are linked to specific roles in the nest context (cf. “specialists” in social insects only perform a few tasks; Robson and Traniello 1999), the optimal ratio of aggressive to non-aggressive workers may differ across tasks, e.g., a trade-off between aggressive competitiveness and emigration tendency. Such cross-contextual performance trade-offs could help to maintain variation in collective personalities and group compositions in situ (Sih et al. 2004; Jandt et al. 2014). In contrast, if worker personality is not linked to their propensity to perform certain nest tasks over others (cf. “elites” in social insects perform many tasks; Robson and Traniello 1999), manipulation of group composition should not significantly influence the efficiency of collective behaviors.

Material and methods

Collection and maintenance

T. curvispinosus were collected in Harpersfield, Ashtabula County, OH, USA, in April 2013. *T. longispinosus* were collected at the Huyck Preserve, Albany County, NY, USA, in early May 2013. Throughout this paper, we refer to ants collected within a single nesting unit as a “colony” (following Modlmeier and Foitzik 2011). Both species were brought to the laboratory at the University of Pittsburgh and kept under identical conditions until the start of the experiment in June 2013. Colonies were kept in artificial nests (7.5×2.5×0.5 cm) in clear plastic boxes (14×13×4 cm) and were provided a continuous supply of water. Colonies were fed ad libitum weekly with pieces of crickets and a droplet of honey. In order to be able to use a split-colony design for our group manipulation, we selected 24 large queenright colonies (12 per species) for our experiment. Further, we ensured that the average number of workers in the source colonies did not differ between the two species (Mann-Whitney *U* test (MWU test): $p=0.71$; $n=12$ per species). The average colony size of these colonies was 130.25 ± 28.26 workers for *T. longispinosus* and 141.58 ± 39.63 workers for *T. curvispinosus*.

Worker characterization

In order to distinguish whether workers could be considered aggressive or docile, we performed individual aggression assays by confronting workers separately with a freshly defrosted conspecific opponent in a small circular arena (diameter=12 mm, height=3 mm), following the methods described in Modlmeier and Foitzik (2011). We used a dead opponent to exclude any effects of the opponents’ behavior on the focal worker (Crosland 1990; Roulston et al. 2003), and because an earlier study had shown that aggression against freshly defrosted opponents is positively correlated to aggression against live opponents (Modlmeier and Foitzik 2011). Opponents were taken from colonies with at least 1 km distance from the focal colony and reused three consecutive times. A worker was considered aggressive if she displayed at least two aggressive interactions in the 15 observations (scan sampling was performed every 20 s for 5 min) or any stinging behavior, workers that showed no aggression were considered docile. We further calculated an aggressiveness score for each worker as the number of times a worker was aggressive divided by the total number of observations (i.e., a score between 0 and 1). Worker aggressiveness scores are highly repeatable on the individual ($r=0.64$) and colony level in *T. longispinosus* ants (Modlmeier et al. 2012; Keiser et al. in review). Workers were kept in Eppendorf tubes until they could be assigned to a group. Surplus workers were returned to their original colony.

Repeatability of individual aggressiveness

To ensure that *T. curvispinosus* workers show similarly high repeatability in aggressiveness as *T. longispinosus* (Keiser et al. in review), we measured a subset of individuals ($n=30$) from 10 randomly selected queenright *T. curvispinosus* colonies twice a day for 2 days according to the previously described worker characterization experiments. Individuals were observed every 20 s for a total of 10 observations per trial. In-between experiments, workers were kept isolated in 0.5-ml Eppendorf tubes with a piece of damp paper.

Manipulation of group composition

Each ant colony was split into two groups of 20 workers each: (1) a docile (only non-aggressive ant workers) and (2) an aggressive group. In addition to the 20 workers, every group was given 10 larvae from its maternal colony during the first experiment (please see: I. Brood recovery). The aggressive group contained different ratios of aggressive to non-aggressive workers with the number of aggressive workers ranging from 1 to 20 to analyze a broad range of possible group compositions. To describe the different group compositions, we defined two variables: (a) the mean aggression of a

group (i.e., the sum of the individual worker aggressiveness scores divided by 20) and (b) the number of aggressive workers per group. In addition, we made sure that these variables did not differ between the two species (MWU test: $p > 0.32$; $n = 12$ aggressive groups per species). Furthermore, we found no species-specific differences in individual aggressiveness (MWU test: $p = 0.5$; $n_{1/2} = 1,059/1,159$). Since we could not divide a single queen into two groups, all artificially created worker groups were queenless. Although *Temnothorax* workers engage in competition for reproductive status after queen loss in *Temnothorax*, intracolony aggressive interactions are very rare in *T. longispinosus* (Konrad et al. 2012). Nevertheless, to minimize potential effects of queen removal on worker aggressiveness, we decided to keep the experimental procedure as short as possible.

Collective behaviors

To measure and compare the collective efficiency of the different group compositions, all group mixtures were tested separately in the following four collective tasks during a period of 5 days:

I. Brood recovery (day 1)

The first collective task was started on the same day as the individual aggression experiments. For each artificially reconstituted group, we put 10 larvae 3 cm away from a new artificial nest in a plastic box (nest and box were identical to the ones described above) and subsequently released 20 workers (who had been in the Eppendorf tubes so far) into the plastic box next to the nest. As soon as the first worker was in the box, a timer was started. We then measured the time needed to discover the new nest site (discovery time; a nest was considered as discovered if a worker moved its whole body into the entrance of the nest), and the time until all 10 larvae were transported into the new nest (total transport time). Subsequently, we calculated the brood recovery efficiency as total transport time minus discovery time.

II. Colony defense (day 2)

On the next day, collective colony defense was measured by confronting each group with one freshly defrosted conspecific opponent (similar to the methods described in Scharf et al. 2012) from a colony at least 1 km away. After the opponent was introduced and the entrance blocked, we registered all aggressive and neutral interactions with this opponent every 20 s for a total of 5 min (15 total observations). Aggressive interactions included mandible spreading (threat display), biting, stinging, and dragging. The total number of aggressive

interactions was then used as our measure of colony defense.

III. Nest relocation (day 2)

One hour after the colony defense assay was completed, we challenged the groups by destroying their artificial nest by removing the roof and side walls. To examine the nest relocation efficiency, we offered them a new intact nest 3 cm away from their old (destroyed) nest and measured discovery time and total time needed to move all larvae into the new nest. Subsequently, efficiency was calculated by subtracting discovery time from the total time.

IV. Nest reconstruction (day 3–5)

Following the methods described in Scharf et al. (2012), we started the nest reconstruction assay 1 one day after the nest relocation experiment. We widened the entrance from 3 to 13 mm by removing parts of the entrance walls and gave each group 0.5 ml of sand that could then be used by the workers to block parts of the entrance again. After 48 h, a picture was taken using a digital camera attached to a stereomicroscope (Leica® Application Suite, version 3.8; Leica, Germany). To estimate the efficiency of nest reconstruction, we drew a line through the area most covered with sand (i.e., the wall built by the workers) and measured the proportion of this line covered with sand. All digital measurements were performed by the same observer (A.P.M.) after all experiments had been completed.

Statistical analyses

Due to the collinearity of mean aggression and number of aggressive workers in both species (Spearman's $r > 0.97$, $p < 0.0001$, $n = 24$ per species), we performed separate analyses for these variables. We first performed omnibus multivariate analysis of covariance (MANCOVAs) on the combined datasets for each species including all colony-level response variables. We included colony identity as a fixed effect in our models and either mean aggression or the number of aggressive workers as covariates. Following a significant combined model, we performed exploratory univariate analysis of covariance (ANCOVAs) for each response variable, in order to analyze whether group composition (“mean aggression” and “number of aggressive workers”) or colony identity influenced each collective behavior. Throughout these tests, we used q values to control for multiple testing (Storey 2002). The q value of a test measures the proportion of false positives incurred (false discovery rate) when that particular test is statistically significant. In other words, the q value can be seen as a minimum p value at which a test may be called

significant. If the residuals of any variable deviated from normality or the variances were heteroscedastic, we used log and/or square-root transformations. However, transformations of the nest reconstruction variable failed to satisfy the assumptions of the homogeneity of variances in *T. longispinosus*, so we resorted to non-parametric tests in this case: we first checked for the effect of colony identity, and because it was not significant (Kruskal-Wallis test: $p=0.49$), we performed Spearman-rank correlations between colony composition variables and nest reconstruction. To calculate repeatability of individual aggressiveness, we performed a GLMM with colony ID as a random effect and individuals nested within colonies as a standard effect.

Results

Repeatability of individual aggressiveness

Aggressiveness in individual *T. curvispinosus* workers was highly repeatable ($F_{20,90}=2.45$, $p=0.002$, repeatability=0.56).

T. longispinosus

The MANCOVAs predicting colony-level behavior were highly significant both for the number of aggressive workers (Wilk's Lambda=0.005, $F_{3,27.31}=3.67$, $p<0.001$) and mean aggression (Wilk's Lambda=0.007, $F_{3,27.31}=3.67$, $p<0.001$). Higher mean aggression resulted in an augmented colony defense behavior (ANCOVA: $F_{1,11}=5.34$, $\beta=0.35$, $p=0.04$, $q=0.05$). Similarly, the number of aggressive workers in a group increased colony defense, although this was only a trend ($F_{1,11}=4.61$, $\beta=0.28$, $p=0.055$, $q=0.06$; Fig. 1). Mean aggression was not associated with nest relocation ($p=0.31$), but having more aggressive workers resulted in faster nest relocation ($F_{1,11}=5.90$, $\beta=-0.23$, $p=0.03$, $q=0.05$; Fig. 2). In contrast, brood recovery efficiency was neither influenced by mean aggression and number of aggressive workers ($p>0.86$) nor by nest reconstruction (Spearman correlations: $p>0.39$). Except for nest reconstruction, all measured collective behaviors in *T. longispinosus* were influenced by source colony identity (ANCOVAs: $F_{11,11}=3.54-9.60$, $p<0.03$).

T. curvispinosus

Neither omnibus MANCOVA was significant for *T. curvispinosus*. Neither the number of aggressive workers (Wilk's Lambda=0.02, $F_{4,38.86}=1.13$, $p=0.36$) nor the mean group aggression was associated with any of our collective

behaviors (Wilk's Lambda=0.02, $F_{4,32.56}=1.31$, $p=0.21$). Thus, we did not continue with any univariate analyses.

Discussion

Here, we were able to demonstrate that group composition, i.e., the mixture of individual personalities within a group, influences at least two different collective behaviors (i.e., colony defense and nest relocation) in *T. longispinosus* ants. Although earlier studies have linked group composition to some measures of collective behavior (Pruitt et al. 2013; Brown and Irving 2014), only a few have disentangled the causal relationship via a manipulation of group composition (Dyer et al. 2009; Chang and Sih 2013). For *T. longispinosus*, we found that colonies composed of more aggressive workers and in which mean aggression was higher also tended to behave more aggressively in colony defense. Additionally, *T. longispinosus* colonies with more aggressive workers were faster at relocating their nest following a disturbance. Thus, in *T. longispinosus*, having more aggressive workers appears to confer multiple benefits. We also detected a significant effect of source colony identity for almost all aspects of collective behavior in *T. longispinosus*. In contrast, we failed to detect any effect of group composition or source colony identity on the collective behavior of *T. curvispinosus*. Collectively, our results suggest that the effects of group composition on collective behavior can be pronounced and varied in nature but can also vary acutely among even closely related and superficially similar species.

Our result that average worker aggression and number of aggressive workers improve colony defense in *T. longispinosus* supports the first and second hypothesis by Pinter-Wollman (2012). That is, colony personality is shaped by the average worker behavior of a colony (H1) and its behavioral distribution (H2). It further suggests that average worker aggression and number of aggressive individuals is partly responsible for between-group differences in colony defense in *T. longispinosus* and possibly other social species (Crosland 1990; Jandt et al. 2014). This is in line with a recent study on social spiders (*Anelosimus studiosus*) demonstrating that aggressive spiders improve colony defense against heterospecific spiders that infiltrate colonies (Pruitt and Riechert 2011a). However, our result that colony defense in *T. curvispinosus* was not altered by changing the group composition shows that there could be fundamental differences in the regulation of colony defense across closely related species. Source colony identity also influenced colony defense in *T. longispinosus*, which indicates that docile workers show similar but weaker colony defensive abilities than their aggressive sisters taken from the same source colony (Fig. 1). Furthermore, docile workers might behave more aggressively

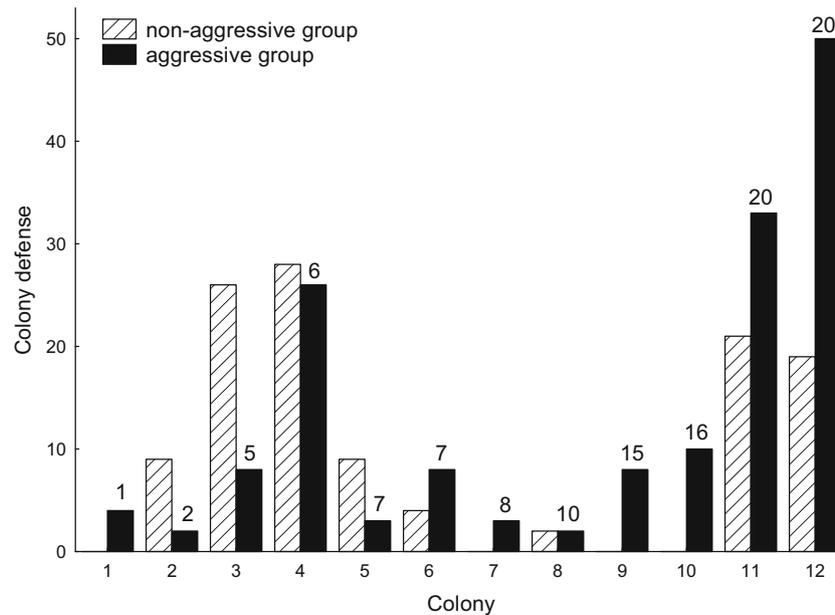


Fig. 1 Collective colony defense for 24 experimentally reconstituted groups of *Temnothorax longispinosus* ants by colony origin depicting the total number of aggressive interactions against a conspecific intruder in a 5-min scan sampling assay. Groups were created by splitting 12 ant colonies into two equally sized groups of 20 workers each: a docile group

(cross-hatched bar) containing only non-aggressive workers or an aggressive group (black bar) with different ratios of aggressive and docile workers: the number next to each black bar represents the number of aggressive workers (1–20 min-max) in the aggressive group. Please see [supplementary material](#) for figures regarding *T. curvispinosus*

while they are together in their own nest than when they are alone in a neutral arena (Tanner and Adler 2009), especially if they originated from an aggressive source colony. Whether or not individuals respond to the presence/behavior of other

group members could strongly depend on the individuals' personality and/or experience (Kurvers et al. 2012; Nakayama et al. 2013). Thus, we reason that other metrics of individual and colony-level personality like social facilitation or numerical

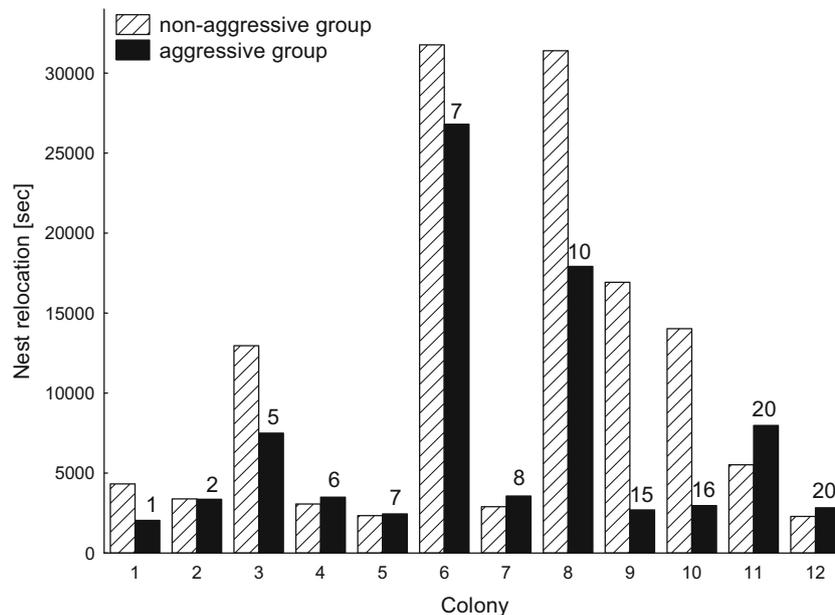


Fig. 2 Nest relocation efficiency for 24 experimentally reconstituted groups of *Temnothorax longispinosus* ants by colony origin. Nest relocation efficiency was measured as the total time needed to relocate 10 larvae into a new nest after disturbance minus the time needed to discover the new nest. Groups were created by splitting 12 ant colonies into two

equally sized groups of 20 workers each: a docile group (cross-hatched bar) containing only non-aggressive workers or an aggressive group (black bar) with different ratios of aggressive and docile workers: the number next to each black bar represents the number of aggressive workers (1–20 min-max) in the aggressive group

assessment (Tanner 2006) could play key roles in the regulation of collective behaviors. A variety of studies have shown personality differences at the colony level in social insects (see Table 2 in Jandt et al. 2014), yet our study is unique in that even when colonies were split into docile and aggressive groups, the source colony remained a significant predictor in one of the two species.

It is surprising that some of the docile groups showed collective aggression levels that were comparable or sometimes even higher than their corresponding aggressive group. One likely explanation could be that even high repeatability scores of 0.5 or higher do, by definition, not explain 100 % of the observed variation. Hence, workers that are docile in one trial might still show aggression in later trials. Since we only tested workers once (more trials per individual would not have been feasible), it is likely that a few workers were classified as docile, despite being aggressive and vice versa. However, the quite high repeatability scores for both species ($r=0.56$ and 0.64) and the fact that our group manipulation had significant effects on colony defense and nest relocation in *T. longispinosus* support our claim that our single aggression experiments were still valid predictors of individual personality.

While the positive effect of a more aggressive group mixture on colony defense was expected and suggested by previous studies (Crosland 1990; Modlmeier and Foitzik 2011), the concurrent positive effect on nest relocation efficiency is surprising. Based on previous findings in the acorn ant *T. nylanderii* (Scharf et al. 2012), we expected to find a trade-off between aggressiveness and emigration abilities like nest relocation efficiency. While the effect of source colony identity on nest relocation efficiency is very clear in Fig. 2, the increase of relocation speed is less obvious. Many aggressive and docile group pairings (from the same colony) show a very similar nest relocation speed. However, when pairings differed strongly in speed, the aggressive group was faster in nest relocation in almost all cases (all but 1 out of 12 pairings). At least in *T. longispinosus*, our results suggest that there could be highly active/aggressive workers, so-called elites (Oster and Wilson 1978; Dornhaus 2008; Dornhaus et al. 2008) that readily perform various tasks, including colony defense and nest relocation. This raises the question: why are not all workers in *T. longispinosus* aggressive, given that aggressive workers improve both colony defense and nest relocation efficiency? A recent study on *Temnothorax rugatulus* demonstrated that colonies with higher levels of aggressive behavior exhibited a lower foraging activity (Bengston and Dornhaus 2014). In *T. longispinosus*, annual per capita productivity increases with within-group variation in aggression suggesting that it is better to have a diverse group mixture and not fully aggressive colonies (Modlmeier and Foitzik 2011). However, slavemaking queens of the ant species *Protomognathus americanus* that try to invade

T. longispinosus nests favor more aggressive colonies (Pamminger et al. 2012). Thus, taken together, in *T. longispinosus* colony composition appears to be under strong selection from a diverse set of ecological pressures. In contrast to *T. longispinosus*, group composition had no detectable effect on the collective behavior of *T. curvispinosus*. This finding suggests that task participation and/or aptitude is either more flexible or that aggressive and docile workers are evenly distributed across tasks in this species.

Why our two species of ants differed so fundamentally in their relationships between group composition and collective behavior remains unknown. One possible explanation is that these species have followed dramatically different evolutionary trajectories, because they must cope with different ecological challenges. For instance, the co-evolutionary arms race between slavemaking ants (*P. americanus*) and their hosts is more advanced in the New York community than the one in Ohio (Brandt and Foitzik 2004). Since *T. curvispinosus* were collected in Ohio and *T. longispinosus* in New York, we might expect the latter species to be more effective in colony defense and brood rescue. Exposure to more intense species interactions has been associated with the emergence of behavioral syndromes in several solitary organisms (Bell and Sih 2007; Dingemanse et al. 2007; Sweeney et al. 2013), and thus, we reason similar relationships may hold for colony-level personality.

Here, we were able to demonstrate that in *T. longispinosus* colonies, colony defense and nest relocation efficiency are influenced by the individual personalities of its workers, whereas in the related *T. curvispinosus*, these behaviors are not. In contrast to earlier studies that found correlative links between individual personalities and collective behavior (Pruitt et al. 2013; Brown and Irving 2014), we directly manipulated the mixture of behavioral types within a group demonstrating that collective behavior can be influenced by the individual personalities of its group members. Interestingly, we also found species-specific differences in the effect of group composition on colony-level behavior: group composition had pronounced effects on some of the collective behaviors of *T. longispinosus* but not *T. curvispinosus*. Similarly, source colony identity only influenced collective behaviors in one of the two species, i.e., in *T. longispinosus*. This suggests that the mechanisms regulating collective behaviors via individual differences in behavioral types might differ strongly among closely related species. We urge that more studies are needed to understand how collective behaviors are influenced by individual behavioral variation in different species. As recently suggested by Jeanson and Weidenmüller (2013), a promising future direction would be to study the evolution of such differences using information from phylogenetic trees to compare the relationship between group composition and collective behavior across related species (Harvey and Pagel 1991).

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