

Original Article

Productivity increases with variation in aggression among group members in *Temnothorax* ants

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Social insect societies are characterized not only by a reproductive division of labor between the queen and workers but also by a specialization of workers on different tasks. However, how this variation in behavior or morphology among workers influences colony fitness is largely unknown. We investigated in the ant *Temnothorax longispinosus* whether aggressive and exploratory behavior and/or variation among nest mates in these behavioral traits are associated with an important fitness measure, that is, per worker offspring production. In addition, we studied how body size and variation in size among workers affect this colony fitness correlate. First, we found strong differences in worker body size, aggression, and exploration behavior among colonies. Most notably, intracolony variance in aggression was positively correlated with per worker productivity, suggesting a selective advantage of colonies with a higher variability in worker aggression. Because ant colonies in dense patches were both more aggressive and more productive, we cannot exclude the possibility that higher productivity and greater variability in aggression could both be results of good habitat quality and not causal influences on one another. This study suggests that social insect societies with stronger behavioral variation among nest members, and possibly a more efficient task allocation, are more productive in the field. *Key words*: aggression, competition, division of labor, fitness, habitat quality, natural selection, personality, social insects, *Temnothorax*. [*Behav Ecol* 22:1026–1032 (2011)]

INTRODUCTION

The ecological success of insect societies can be largely attributed to their division of labor (Wilson 1987; Hölldobler and Wilson 1990). The primary division of labor is that between the reproductive caste—the queen—and the usually sterile workers. Tasks are further subdivided among the workers, often resulting in morphological or temporal castes (Hölldobler and Wilson 1990). Division of labor is characterized by 2 principal components: 1) simultaneous performance of multiple activities by different individuals and 2) the specialization of individuals on one activity over some meaningful time frame (Oster and Wilson 1978; Robinson 1992). Why this specialization evolved is still unclear. One general assumption was an increased individual efficiency through task specialization. Surprisingly, this was not supported by empirical data from *Temnothorax* ants, which showed that specialization does not necessarily increase individual efficiency (Dornhaus 2008). As Chittka and Müller (2009) pointed out, empirical evidence remains scarce that division of labor and task specialization are increasing colony efficiency. Therefore, studies on the intracolony variation in behavior and its fitness benefits for the colony are needed to understand the evolution and maintenance of division of labor, one of the most characteristic traits of social insects.

According to the response threshold models (reviewed in Beshers and Fewell 2001), division of labor and its individual task specialization are generated by variation in response thresholds among workers within a colony. Workers will perform a task if the corresponding stimulus exceeds their internal threshold (Bonabeau et al. 1996). Specialists are therefore workers who have a lower threshold for a specific task and a higher threshold for other tasks. Consequently, task specialists represent distinct behavioral types of a colony. The term “behavioral type” has not been used in the social insect literature but has been coined to describe consistent multidimensional behavioral variants in nonsocial animals. In recent years, animal species that show this consistent behavioral variation have been described to exhibit personalities or behavioral syndromes (Sih et al. 2004). Studying behavioral variation in relation to reproductive success can yield valuable insights into the direction and intensity of natural selection on behavioral traits. According to a recent meta-analysis, personality dimensions such as aggression, exploration, and boldness were found to have important fitness consequences in many different species (Smith and Blumstein 2008). We expect to find similar effects in ants where consistent variation in behavior and social organization of colonies can have a genetic basis (Stuart and Page 1991; Ross and Keller 1998). There is, however, an important difference between social insects and solitary species. In contrast to solitary animals, natural selection in social insects can also act on the colony level (Korb and Heinze 2004). The importance of group selection for the evolution of eusociality is currently controversial (Nowak et al. 2010; Okasha 2010). In addition to between-colony variation in behavior, resulting in

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behavioral types of colonies, insect societies could also differ in the variation within the colony, that is, the number and distinctness of behavioral types present within a colony.

Many studies on animal personalities include variation in exploration behavior (Verbeek et al. 1994; Dingemanse and Réale 2005). Although exploratory animals have a higher chance to discover food sources, they also take higher risks and have higher metabolic rates (Careau et al. 2008). As a consequence of their more active and exposed lifestyle, they consume more energy and are prone to predation. Another personality dimension, aggression, plays a fundamental role in nest defense and in the competition for resources or nest sites (Collias 1944; Kontiainen et al. 2009). The effect of worker aggression on colony fitness under field conditions has not been explored so far. Although aggressive behavior may help in acquiring and defending resources, it involves apparent costs, including higher metabolic rates and the risk of injury or death (Holway et al. 1998; Gobin et al. 2003). Furthermore, time and energy spent fighting cannot be used for other important social interactions, such as brood care.

Social insects provide the opportunity to study the benefits of behavioral variation for animal groups. In insect societies, specific individuals can become allocated to certain tasks, leading to a high variance of behavioral types among nest mates and consequently to a strong division of labor. This variation could be particularly beneficial when behavioral uniformity is costly. For example, under high-density conditions, colonies with a higher variability in aggressive behavior could be favored by natural selection: Whereas the aggressive behavioral types defend the colony, less aggressive nest mates care for the brood. We therefore predict that high variation in worker behavior should improve colony productivity. We tested this prediction in the ant species, *Temnothorax longispinosus*, which was already known to exhibit a clear division of labor (Herbers and Cunningham 1983). We investigated whether aggressive or exploratory behavior and variation among nest mates in these traits were associated with a measure of fitness (i.e., per worker productivity of a colony). Brood production in *Temnothorax* ants is highly synchronized, and we collected ant colonies shortly before the emergence of the new workers and sexuals. Hence, the observed offspring production should be a reliable assessment of the total annual production (Headley 1943; Kipyatkov 1993).

Aside from behavioral variation, morphological variation may also contribute to the productivity of ant colonies. First, task performance can be linked to the body size of workers. One of the most extreme cases of size variability among workers (by the factor 6, based on head width measurements) can be found in leafcutter ants of the genus *Atta*. In these fungus-growing ants, smaller workers focus on the maintenance of the fungus garden, mid-sized workers degrade leaves and carry the fragments back to the nest, and the largest worker castes are involved in cutting of the vegetation (Wilson 1980b). Maintaining this variability in worker sizes within colonies of polymorphic ant species is not only important for worker survival (Billick and Carter 2007) but also for brood production (Porter and Tschinkel 1985; Billick 2002). Second, worker size in social insects can be associated with task efficiency, described as superior performance under normal conditions (Couvillon and Dornhaus 2010). Support for this hypothesis comes from bumblebees where larger workers collect more nectar per unit time (Goulson et al. 2002; Spaethe and Weidenmüller 2002). In contrast, smaller workers are more resistant to starvation and are presumably cheaper to produce (Couvillon and Dornhaus 2010). Despite being generally monomorphic, workers of our focal ant *T. longispinosus* vary in size by the factor 1.3 in head width within a colony (Figure 1a), and this variation is related to their behavioral

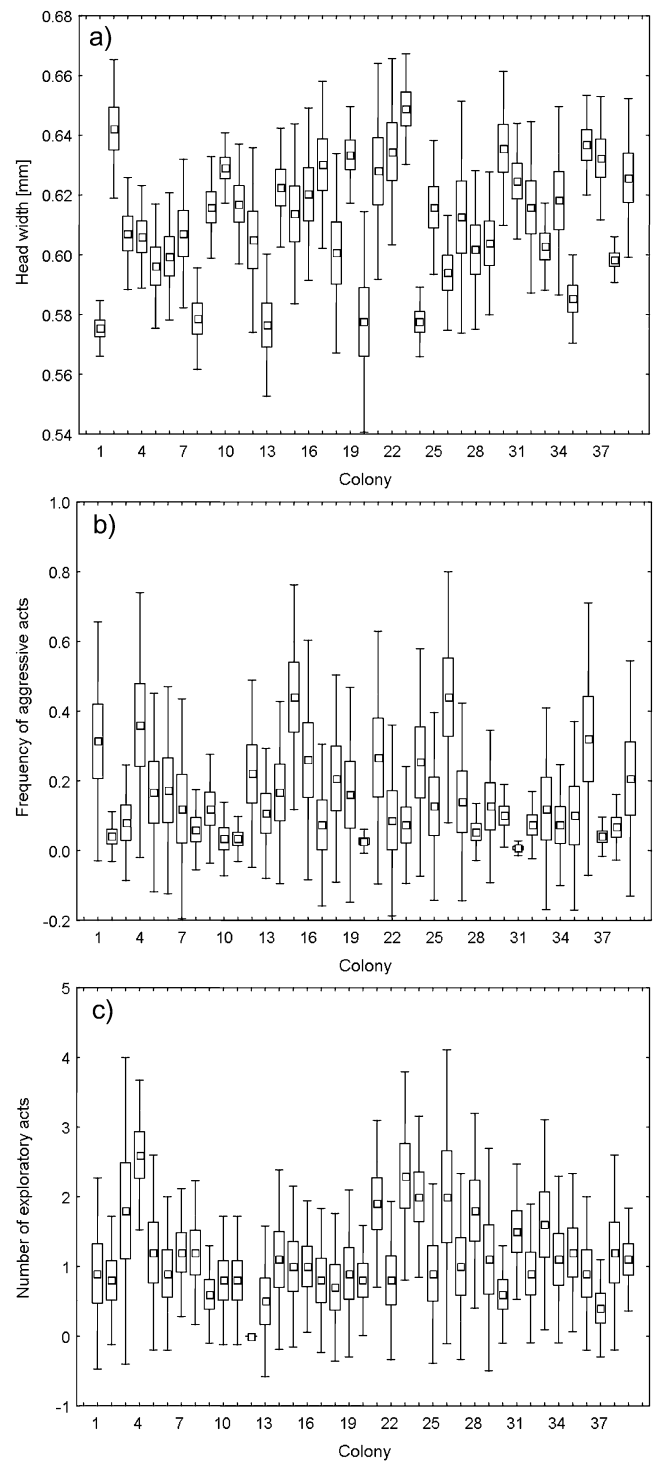


Figure 1
Differences in (a) mean colony head width, (b) aggressive behavior, and (c) exploratory behavior among 39 colonies of *Temnothorax longispinosus* from a study site in upstate New York, USA. Ten workers per colony were tested. Results are shown as means with the box showing standard error and the brackets showing SD.

caste (Herbers and Cunningham 1983). It is unclear whether size also determines task efficiency and ultimately colony fitness in ant species with monomorphic workers and a much lower variation in worker body size. Therefore, the second part of this study will investigate whether worker body size and its variation influence colony productivity.

In social insects, per worker productivity was shown to decrease with colony size ("Michener's paradox," Michener 1964), and this relationship was thought to oppose the evolution of large insect societies. However, recent studies found varying relationships between colony size and productivity, including positive, negative, and no clear relationships (for references, see Dornhaus et al. 2008). Hence, colony size, that is, worker number, can certainly influence colony fitness. Furthermore, productivity is not only affected by colony characteristics but also by ecological conditions, such as food availability and competition. In ants, nest density can reflect local habitat quality and is often associated with intraspecific competition (Hölldobler and Wilson 1990). In dense patches, foraging ants frequently encounter intraspecific competitors, which can cause adaptive increases in the aggression level (Thomas et al. 2007; Van Wilgenburg et al. 2010). Therefore, we analyzed whether nest density was associated with higher aggression levels and/or a higher productivity in the nonterritorial *T. longispinosus* ants.

The central hypothesis of this study was that behavioral and morphological variation among group members contributes to fitness in ants. Specifically, we test these 2 predictions: 1) Intracolony variation in aggressive and exploratory behavior improves colony productivity and 2) intracolony variation in worker size improves colony productivity.

MATERIALS AND METHODS

Study system

Our study species, *T. longispinosus*, lives in mixed deciduous forests across the northeastern United States and inhabits preformed cavities in acorns, hickory nuts, and twigs. Although these ants are facultatively polygynous and polydomous, most colonies at our study site in New York contain a single queen and a single nesting unit (Foitzik et al. 2004). Only about 10% of all nests have several queens (data from Foitzik et al. 2009 based >750 nests). Polydomy is relatively rare as genetic analyses (Foitzik et al. 2004) showed that 10.7% of all colonies were polydomous, each consisting of 2 or 3 subunits. We did not genotype all colonies (and the surrounding nests), so that we cannot rule out that some of the colonies included in our analyses were indeed polydomous. We decided to analyze the data on the level of the local nest unit because selection was suggested to act on the nest level in this species (Herbers and Stuart 1996).

Colonies were collected in oak-hickory forests at the Huyck Preserve, Albany County, NY (USA), between 10 AM and 5 PM in early August 2009, at a time of the day during which foraging is ongoing. *Temnothorax* ants forage solitary, and less than 10% of all workers leave the nest for foraging at any one time (Foitzik S, personal observation). We estimate that we have missed 1–5 workers per nest depending on its size. However, this fraction should be similar for all colonies as we only collected nests during the active foraging period. At the time of collection, ant colonies contained sexual and worker brood shortly before emergence from the pupae. Ant colonies were censused at the field station within days of collection and transported to the laboratory in Munich (Germany), where they were transferred to artificial nests in 3-chambered plastic boxes (9.5 × 9.5 × 2.7 cm) with a moistened plaster floor. Ants were fed twice weekly with honey and pieces of dead crickets.

We included only well-established monogynous colonies with at least 20 workers in all experiments ($n = 39$ colonies, mean worker number = 44.69, standard deviation (SD) = 20.83). Thereby, we reduced the impact of colony size and eliminated potential effects of queen number on worker behavior or per capita productivity. All behavioral experiments were conducted

by the same person (A.P.M.) in the laboratory in Munich between 31 August 2009 and 17 October 2009. Behavioral experiments were started 2 weeks after collection in the field.

Per capita productivity

We used total biomass production divided by the number of workers (per capita productivity) as a measure of fitness. In *Temnothorax* ants, the different castes, that is, queens, workers, and males, vary in size and biomass. The average dry number of *T. longispinosus* queens is 873.4 µg, whereas workers and males weigh only 216.6 and 231.1 µg, respectively (Foitzik et al. 2004). Hence, total offspring production of a colony was calculated by multiplying the total number of worker, male, and queen pupae with the respective mean values of dry number for adult workers, males, and virgin queens as previously determined for colonies collected at the same site (Foitzik et al. 2004). Early-stage pupae, so-called prepupae, whose caste could not be reliably determined were included in the analyses as worker pupae. Per capita productivity was calculated by dividing the total dry mass production of a colony by the number of adult workers residing in the ant nest.

Competition and nest density in the field

To investigate how ecological conditions (especially competition) affect ant behavior, we analyzed colony density in the field. Thirty-five of the 39 colonies were taken from 6 × 3 m study plots, which were carefully searched for all ant colonies. The positions of all *T. longispinosus* colonies within these plots were recorded. In addition, we mapped the position of all colonies of the slave-making ant, *Protomognathus americanus*, which contained enslaved *T. longispinosus* workers. The latter colonies were included in the evaluation of nest density because *Temnothorax* slaves take over the foraging task in these colonies and thus directly compete with foragers from unparasitized colonies. *Temnothorax* workers are only 2–3 mm in length. For the congeneric species, *T. nylanderii*, the mean foraging distance was determined to be below 20 cm (Heinze et al. 1996). We therefore were interested in nest density in the immediate vicinity of each nest. The 6 × 3 m study plots were divided into 72 squares of 50 × 50 cm. Local density was subsequently determined for each colony by counting the number of ant nests in the same square and in the 5 closest squares inside the study plot. We used squares instead of density within a given distance because thereby we avoided extrapolation for colonies located at the plot border. We estimated the nest density for the 4 colonies outside of the plots by using average densities per 1.5 m² of the closest study plots.

Order of experiments

We randomly selected 10 workers per colony that were used throughout all experiments. Workers were tested for exploration first and followed by an aggression test. In-between experiments, workers were kept separately in Petri dishes (diameter 33 mm and height 11 mm) with a wet piece of paper for approximately 1 h. After the aggression experiment, workers were frozen for the morphological analysis.

Aggression experiments

In order to estimate mean aggression and intracolony variance in aggressive behavior, 10 workers per colony were tested separately. Each worker was transferred to a small circular arena (diameter 12 mm and height 3 mm) with a freshly defrosted dead conspecific from 1 of 8 queenright colonies from a population in West Virginia. Because *Temnothorax*

colonies contain on average less than 50 workers, we had to use opponents from several colonies. Variation in chemical profiles of opponents from different colonies could lead to variance in aggression. To eliminate this possibility, we used for a single test colony always dead workers from the same colony. By using a dead adversary, any effects of the opponents' behavior could be excluded (Crosland 1990; Roulston et al. 2003). However, to ensure that experiments with dead opponents reflect aggression of workers also in live encounters, we performed additional experiments with laboratory *T. longispinosus* colonies. We marked 8 workers per nest and tested them individually 3 times against a single-living conspecific worker from a different colony to get a good estimate of their average aggression. Subsequently, each worker was tested a fourth time, but the opponent in this test was a dead conspecific worker. In-between experiments, marked workers were returned to their original colony for 1 week. These experiments confirmed that individual aggression against dead ants significantly correlates with the average aggression of repeated tests against living ants (Spearman's rank correlation: $r_s = 0.45$, $P < 0.001$, $n = 52$ workers).

We calculated the proportion of aggressive behavior of a worker by recording its behavior every 20 s over 5 min and then dividing the number of aggressive interactions by the total number of observations. Aggressive interactions included mandible opening (threat display), biting, dragging, carrying, and stinging. For further analysis, we used mean and SD over 10 different workers from each colony as a measure of the level and the variation in behavior within the colony. We used the SD as a measure of the behavioral variation within colonies instead of the variance because the latter is more prone to be influenced by outliers.

If a dead opponent was not attacked, we reused it in up to 4 trials. We tried to ensure that the chemical profile of these reused opponents did not change. First, we did not reuse opponents that were physically attacked by biting and stinging. Second, each experiment lasted only 5 min plus approximately 3 min for preparation. Thus, dead opponents were kept less than 40 min outside of the freezer. Third, we always tested the 10 workers of a colony on a single day. Every colony started with a new (unused) opponent and had therefore the same chance of being tested against unused workers. We wiped the arena carefully with ethanol after each trial to eliminate potential residual odors.

Exploration experiments

We used a multichamber setup to test exploratory behavior. The experimental setup consisted of a central chamber (diameter 29 mm and height 3 mm) that was connected to 8 equally sized side chambers through 8 corridors (length 32 mm and width 7 mm). Each of the 8 chambers contained a different, unknown but chemically distinct object, mainly spices: dried pieces of spruce needles, oregano, caraway, thyme, rosemary, sage, chamomile, and savory. When an ant was released in the central chamber, we recorded for 5 min how often it would antennate these unknown objects. A single antennation event started when the worker touched one of the unknown objects with its antennae. If the contact was interrupted for more than 1 s, a new antennation was counted. We used the mean and SD of the number of antennations over the 10 different workers from each colony as a measure of the level and the variation in exploratory behavior within each colony. After each experiment, we entered new objects and wiped the arena with ethanol.

We used the term "exploratory behavior" following Verbeek et al. (1994) and Réale et al. (2007), who classified both the exploration of novel environments and of novel objects as

exploratory behavior. We chose to use the number of antennations as a measure of exploratory behavior because a possible alternative measure, the number of chambers that an ant investigated, would be strongly influenced by the activity level of the ant. Individuals ants could just by running around enter many chambers and not because they behave very exploratory. In contrast, antennation is a better measure of interest for a novel object.

Worker size

In order to estimate mean worker size and variation in a colony, the head width of 10 workers per colony was measured to the nearest 0.01 mm with an ocular micrometer. Head width is the most commonly used character to estimate worker size in ants (Wilson 1980a; Herbers and Cunningham 1983).

Statistical analyses

We used Kruskal–Wallis tests to check for differences in behavior or morphology between colonies. In order to analyze which parameters were associated with behavioral or morphological differences among colonies, we performed stepwise multiple regressions with mean colony aggression or exploration as dependent variables. The multiple regression model was selected in a backward stepwise process, first including all explanatory variables and then removing factors until the highest adjusted r^2 value was reached. Explanatory variables for both behavioral traits were colony size (N of adult workers), mean colony head width, SD of colony head width, relative colony productivity (dry number production per worker), and nest density. Additionally, we included mean exploratory behavior as an explanatory variable for mean aggression and accordingly mean aggression as an explanatory variable for exploratory behavior.

Finally, we wanted to investigate if variation in aggression, exploration, and body size can explain the analyzed fitness component, that is, the relative productivity of a colony. Therefore, we performed a second backward stepwise multiple regression but this time with the relative productivity as the dependant and the number of adult workers, mean colony head width, SD of colony head width, mean colony aggression, SD of colony aggression, mean colony exploration, SD of colony exploration, and nest density as explanatory variables. For the regression analyses, normality of residuals was tested with Kolmogorov–Smirnov tests ($P > 0.2$). Homogeneity of variances was checked graphically by plotting the residuals against the values of the explanatory variables.

RESULTS

Colonies differed strongly in worker size, aggression, and exploration behavior (Kruskal–Wallis tests; worker size: $H_{38,390} = 170.28$, $P < 0.0001$, Figure 1a; aggression: $H_{38,390} = 78.66$, $P < 0.0001$, Figure 1b; and exploration: $H_{38,390} = 69.56$, $P < 0.002$, Figure 1c).

Next, we explored colony-level variation in behavior and morphology. The final regression model ($F_{2,36} = 4.97$; $P < 0.013$; $r^2_{\text{adjusted}} = 0.17$; Supplementary Table S2b), which explained most of the differences in mean aggression among colonies, included nest density ($b = 0.388$, $P < 0.014$) and mean exploration ($b = 0.217$, $P = 0.152$). Colony aggression increased with nest density (Figure 2). Differences in mean colony exploration could not be explained by any of the independent factors, including the nest density, colony size, head width, aggression, and productivity. The best regression model (Supplementary Table S3b) included only mean aggression and SD of head width and was not significant (Stepwise multiple regression: $F_{2,36} = 2.65$; $P < 0.09$; $r^2_{\text{adjusted}} = 0.08$).

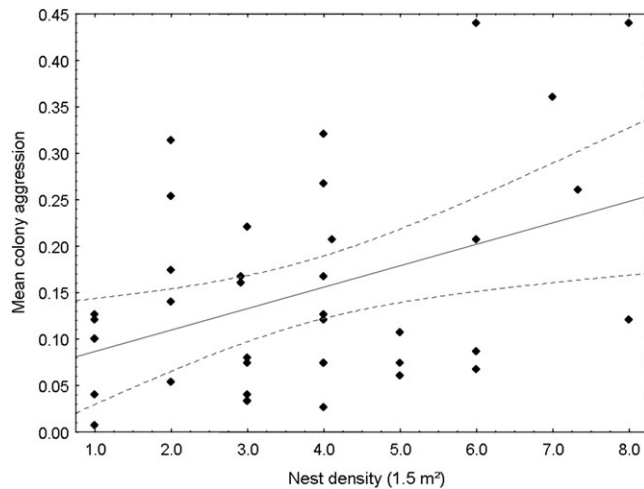


Figure 2 Positive relationship between nest density (1.5 m^2) and the mean colony aggression in 39 tested colonies of *Temnothorax longispinosus* from a study site in upstate New York, USA. Figure includes 95% confidence bands.

Colony productivity was positively associated with the SD of aggression (backward stepwise multiple regression: $b = 0.544$, $P = 0.029$; Figure 3a) and the number of neighboring colonies ($b = 0.487$, $P = 0.004$; Figure 3b, Table 1). Hence, colonies with a higher SD in aggression and in denser areas showed a higher relative productivity.

DISCUSSION

The results of this study revealed that the productivity of ant colonies increased with intracolony variation in aggressiveness, which suggests a selective advantage of behavioral variation among group members. These colonies might be more productive because tasks such as nest defense and brood care are taken over by specialized workers with different thresholds. Whereas workers with a low threshold for aggressive responses engage in competitive interactions with other colonies, less aggressive social workers take care of the brood. Albeit variation in worker behavior or in other words in the division of labor is thought to be the basis for the ecological success of social insects, there are very few studies, if any, that show a direct relationship between behavioral variation and colony fitness. What has been shown is that social insect colonies that have a higher genetic diversity among workers show a higher productivity (Cole and Wiernasz 1999; Wiernasz et al. 2004), a better temperature regulation (Jones et al. 2004), and an increased resistance against disease infections (Tarpay and Seely 2006). These positive effects of genetic diversity were interpreted to be the result of a stronger variation in response thresholds in genetically diverse colonies. However, we do not expect strong differences in genetic variability between the *T. longispinosus* colonies tested here because all study colonies were monogynous and this species is also known to be invariably monandrous (Foitzik et al. 2004).

A common problem of laboratory experiments in behavioral ecology is that behaviors can differ between a field and a laboratory setting. Nevertheless, we argue that our laboratory observations, especially those concerning the behavioral differences among colonies, can be used to examine the results in an ecological and evolutionary perspective for several reasons: First, we found that the behavior of the laboratory colonies did not change over the duration of the experiments (August

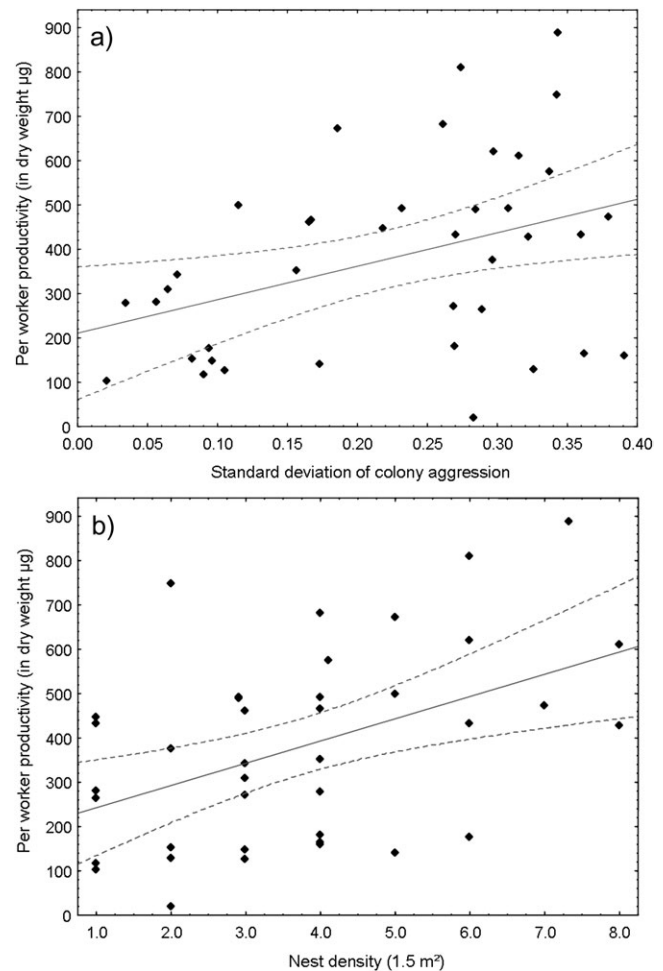


Figure 3 Positive relationship between the fitness component (per worker productivity) and (a) the SD of colony aggression and (b) nest density (1.5 m^2). Thirty-nine colonies of *Temnothorax longispinosus* from a study site in upstate New York, USA, were tested. Figures include 95% confidence bands.

2009 to October 2009). Moreover, we were able to show that the behaviors of *T. longispinosus* colonies (mean aggression and variability in aggression, Modlmeier AP, Foitzik S, unpublished data) are consistent for at least 4–5 months, with a new generation of workers emerging in between the behavioral experiments. Similarly, the aggressiveness of colonies and the number of aggressive workers remained constant in a study on the ant *Rhytidoponera confusa* (Crosland 1990). These findings support the general assumption of response threshold models that behavioral thresholds are fixed and have a genetic basis (Beshers and Fewell 2001). In theory, this could lead to intercolony variation in behavior and thus to personalities on a colony level. Nevertheless, the mechanisms that regulate response thresholds in ants are still poorly understood. Differences between individuals can depend on genotype, age, and experience (Page and Erber 2002). Workers that are successful at one task might show a higher tendency to perform this task again compared with those that failed. Clonal same-aged workers of the parthenogenetic ant, *Cerapachys biroi*, that were allowed to capture prey continued to forage over weeks, whereas unsuccessful workers specialized on brood care and refrained from leaving the nest to forage (Ravary et al. 2007). Consequently, individual experience could also influence exploratory and aggressive behavior in *T. longispinosus*.

Table 1
Results of the best multiple regression model on the relative colony productivity (annual production in dry weight/number of workers) as the dependant variable

Explanatory variable	β	<i>P</i> value
Mean colony aggression	-0.350	0.166
SD colony aggression	0.544	0.029
Mean colony exploration	-0.319	0.087
SD colony exploration	0.195	0.279
Nest density (1.5 m ²)	0.487	0.004
SD of colony head width	-0.166	0.271

The model was selected in a backward stepwise process, first including all explanatory variables and then removing factors until the highest adjusted r^2 value was reached ($F_{6,392} = 3.42$; $P < 0.011$; $r_{\text{adjusted}}^2 = 0.28$). In the original model (Supplementary Table S1) were the following explanatory variables included: the number of adult workers, mean colony head width, SD of colony head width, mean colony aggression, SD of colony aggression, mean colony exploration, SD of colony exploration, and nest density (1.5 m²). Colony behavior was analyzed by testing 10 ant workers per colony separately in standardized experimental setups. A total of 39 colonies were included. Significant *P* values are shown in bold.

Our results show that ecological factors might influence worker behavior. Variation in aggression between colonies could be in part explained by density in the field as the mean aggressiveness of workers from a colony was positively correlated with nest density. In the invasive Argentine ants, contact to intraspecific competitors and fighting experience lead to elevated levels of aggression (Thomas et al. 2007; Van Wilgenburg et al. 2010). Hence, the generally much less aggressive and nonterritorial *T. longispinosus* ants might similarly react to frequent contacts with competitors by increasing the aggression level over longer time periods. In other words, a phenotypic plastic response to crowding at the population level might raise intraspecific aggression. Alternatively or in addition, only aggressive colonies might be able to compete in dense populations with many competitive encounters between neighboring colonies. Albeit *Temnothorax* ants do not defend territories (Heinze et al. 1996), less aggressive colonies might be outcompeted or evicted from their nest sites, which are a main limiting ecological parameter in the *T. longispinosus* population at our New York study site (Herbers 1986). Nest sites of these ants—acorns, hickory nuts, and twigs—decompose during the warm and wet summer months and become limited at the end of the season (Foitzik and Heinze 1998). *Temnothorax* colonies are forced to relocate their nests and might end up close to competing ant colonies. Natural selection could therefore lead to an occupation of high-density areas by aggressive colonies.

Interestingly, the relative productivity of colonies increased with nest density. If intraspecific competition is important in this system, we would have expected an association in the opposite direction namely that productivity decreases with the number of competitors in the vicinity. However, nest density can be a reliable indicator of good habitat quality, which has been shown both in birds (Bock and Jones 2004; Pérot and Villard 2009) and ants (Kaspari et al. 2000). If also true for our system, high habitat quality, that is, food availability, could lead both to a higher ant nest density and a higher productivity of colonies, resulting in the observed positive correlation between nest density and productivity. The main conclusion from this finding would be that habitat heterogeneity is more important for ant colony productivity than competition for food.

This finding also suggests an alternative scenario in which higher productivity and greater variability in aggression could both be results of good habitat quality and not the result of one factor directly influencing the other. Good habitat quality

could lead to higher productivity and higher nest density. The latter could increase not only mean aggression but also intracolony variation in aggressiveness if foragers and scouts engaging in frequent aggressive encounters outside of the nest become more aggressive than ants inside the nest.

As our results suggest a selective advantage of behavioral variation, the question arises why some colonies vary more in their behavior than others. One source of behavioral variability could be intracolony genetic variation. *Temnothorax* queens are generally singly inseminated, but genetic diversity can arise in this species through facultative polygyny. In honey bees, behavioral variability is indeed associated with genetic diversity (Fewell and Page 1993; Page et al. 1995), and the fitness advantage of genetic diversity has been shown in colonies of harvester ants and honey bees, where multiple mating leads to higher productivity and resistance against diseases (Cole and Wiernasz 1999; Tarpay 2003; Wiernasz et al. 2004).

Neither variation nor mean worker body size was associated with per capita productivity. Accordingly, behavioral variability was associated with a measure of fitness, whereas morphological variation was not. Although earlier experiments showed an association between body size and division of labor in *T. longispinosus*, where larger workers were more likely to forage (Herbers and Cunningham 1983), we did not find evidence that morphological variation in this monomorphic species is adaptive.

We uncovered strong intraspecific differences among ant colonies. Colony-level variation was found in worker body size and also in behavior of workers in standardized tests. Similar to the observed personalities in nonsocial animals (Verbeek et al. 1994; Réale et al. 2000), insect colonies appear to exhibit clear behavioral differences with multiple dimensions. Colonies not only differed in a single behavioral parameter but at least in 2-exploration and aggression.

In conclusion, we demonstrate that mean colony aggression increases with nest density, which can be due to natural selection, phenotypic plasticity in behavior, or a combination of both. Regardless of the mechanism, our findings underline the importance of aggression for the reproductive success of animals (Konttinen et al. 2009), especially under high-density conditions. Our result that colony productivity increases with nest density in the New York population of *T. longispinosus* indicates that habitat heterogeneity is more important than competition in this environment. Finally, the key finding of this study, the empirical link between intracolony variation in aggressiveness and per capita productivity, suggests that behavioral variation, presumably leading to a strong division of labor, can increase the fitness of social insect colonies.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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