

## Original Article

# A proactive–reactive syndrome affects group success in an ant species

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Social insects have been particularly evolutionarily successful: they dominate terrestrial ecosystems all over the globe. Their success stems from their social organization, where one or a few individuals reproduce, whereas others carry out different colony tasks. From an evolutionary standpoint, social species are particularly interesting because natural selection acts at both the individual and colony levels. Therefore, we might expect to see selection acting simultaneously on personality at the individual level and colony level. In this study, we tested whether captive colonies of the ant *Aphaenogaster senilis* exhibited different behavioral types and evaluated their consequences for intraspecific competition. Our results demonstrate that colonies of the same age exposed to standardized laboratory conditions did indeed have different personalities. In addition, we found that *A. senilis* demonstrated a behavioral syndrome that included proactive and reactive behaviors: colonies varied in their approaches to exploration, risk taking, food retrieval, and conspecific interactions. This syndrome appears to be associated with a trade-off between competition for food resources and temperature-related foraging risks. “Bold” colonies contained individuals who more readily explored novel environments, exhibited aggressive behaviors, and demonstrated higher food-retrieval efficiency during intraspecific competition trials. However, such colonies were also more risk prone: workers suffered higher mortality rates because they more frequently foraged over their critical thermal maximum. The trade-off we observed under laboratory conditions might be key in maintaining colony-level personality, thus driving local-level adaptations in collective behavior.

**Key words:** *A. senilis*, colony personality, intraspecific competition, proactive–reactive behavioral syndrome, trade-off.

## INTRODUCTION

The concepts of animal personality and behavioral syndromes have challenged long-standing paradigms in the fields of animal behavior and behavioral ecology; for instance, some behaviors appear to be strikingly nonadaptive in specific contexts (e.g., high activity levels in the presence of predators) (Sih et al. 2004; Dall et al. 2012; Wolf and Weissing 2012). Animal personality refers to interindividual behavioral differences that are consistent over time and across different situations, whereas behavioral syndromes are suites of correlated behaviors that are equally consistent (Gosling 2001; Sih et al. 2004; Wolf and Weissing 2012). Variation in individual personality has been observed in a wide range of taxa and is currently considered to be a ubiquitous feature of animal populations (Dall et al. 2004).

From an evolutionary perspective, animal personality has been difficult to explain because flexible behavior should provide a selective advantage. An “optimally designed” animal might be expected

to behave in a certain way only when the situation requires it and should be able to adjust its behavior as conditions change. However, the fact that certain intraspecific behavioral differences persist over time and across varying situations highlights that trade-offs appear to constrain behavioral plasticity and optimality (Krebs and Davies 1997). For example, in a competitive context, proactive individuals—who are consistently more aggressive and bold—may reap more fitness benefits than reactive individuals (Wilson et al. 2013). However, they may also incur higher costs in the form of higher mortality rates because they take more risks in dangerous environments (Smith and Blumstein 2008; Cole and Quinn 2014) or engage in unnecessary confrontations over resources. Alternatively, reactive individuals may avoid dangerous situations; although they may suffer fewer direct injuries, they may also miss out on opportunities to exploit resources (Koolhaas et al. 1999; Sih et al. 2004; Coppens et al. 2010).

Social species are intriguing because natural selection acts at both the individual and group levels (Keller 1999; Korb and Heinze 2004; Eldakar et al. 2010; Chang and Sih 2013). In social species, the group fitness is a nonadditive function of the fitness of its members. This is because the efficiency of collective behaviors such as the retrieval of large prey increases in a nonlinear

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fashion as the number of individuals participating increases (Ruel et al. 2012). Therefore, we may expect to see behavioral syndromes, and personality, evolve not only at the individual level but also at the group level. Polymorphism in group-level behavioral traits has recently been described in many taxa, including fishes (Dyer et al. 2009); birds (Aplin et al. 2013, 2014); and insects such as ants (e.g., Chapman et al. 2011; Gordon et al. 2011; Pinter-Wollman, Gordon, et al. 2012; Scharf et al. 2012; Bengston and Dornhaus 2014; Hui and Pinter-Wollman 2014; Kleeberg et al. 2014; Modlmeier, Keiser, Shearer, et al. 2014), bees and bumble bees (e.g., Wray et al. 2011; Wray and Seeley 2011), and spiders (e.g., Pruitt and Keiser 2014; Keiser, Jones, et al. 2014); reviewed in Jandt et al. (2014) and Kralj-Fišer and Schuett (2014).

An emerging idea in behavioral ecology is that the group's overall behavioral type—that is, the particular configuration of behaviors expressed (Bell 2007)—influences collective behavior and group performance (Webster and Ward 2011). Yet few studies have experimentally tested this idea, despite its ecological and evolutionary implications. In water striders, group composition has been found to impact overall group mating activity (Sih and Watters 2005; Eldakar et al. 2009; Chang and Sih 2013). In social spiders (*Stegodyphus sarasinorum*), collective prey capture is dependent on the relative boldness of group members (Pruitt et al. 2013). Another example comes from guppies: Dyer et al. (2009) created mixed groups of bold and shy individuals. In bold groups, individuals were significantly more likely to enter a feeding area and thus feed first, whereas individuals in the shy groups were more likely to feed second. Similarly, overall group behavioral type influences foraging activity in barnacle geese. Groups containing fewer neophobic individuals were more likely to discover new food patches than groups containing more neophobic individuals (Kurvers et al. 2010).

Several factors that can affect group-level personality traits should be controlled for when studying social species. For example, the level of analysis (individual or group) as well as a colony's age and past experiences have been found to affect group personality (Bengston and Jandt 2014); however, previous studies have failed to control for all these factors in tandem. Although a collective behavior might result from the average behavioral types of its members (Pinter-Wollman 2012), an analytical approach that focuses on individuals may lead to a mischaracterization of group-level personality. Indeed, the presence of a few “keystone” individuals has been observed to shape the collective behavior of whole groups (Modlmeier, Keiser, Watters, et al. 2014; Pruitt and Keiser 2014). Therefore, a group-centered approach should be preferred when studying group personality. Past experiences are another factor that is known to affect collective behavior but that has rarely been controlled for (Bengston and Jandt 2014). For example, if an ant colony has come into repeated contact with a neighboring colony in the past, its members will exhibit greater aggressiveness toward non-nestmates (Knaden and Wehner 2003; Thomas et al. 2006; Kleeberg et al. 2014). A single encounter with a slave-making ant increases colony-level aggressiveness in *Temnothorax* (Pamminger et al. 2011). Finally, colony behavior may change with age. For instance, in harvester ants, older colonies were found to be more stable to perturbation and more homeostatic (Gordon 1987).

In this study, we therefore decided to test whether ant colonies express personalities while controlling for colony age and past experiences. We also examined whether group behavioral type affects collective behavior and group performance. We determined whether our study species, *Aphaenogaster senilis*, exhibited behavioral syndromes related to resource acquisition; namely, we

examined whether ant colonies demonstrated correlated suites of proactive versus reactive behaviors, such as readiness to engage in exploration, boldness, aggressiveness, and risk taking. In addition, we analyzed the relationship between colony-level personality and competitive ability by testing whether the outcome of competitive interactions between colonies could be explained by colony behavioral type. We predicted that high activity levels, aggressiveness, and boldness would give colonies an advantage in competition for resources. We aimed to better understand the role played by personality traits in driving the competitive performance of groups.

## MATERIAL AND METHODS

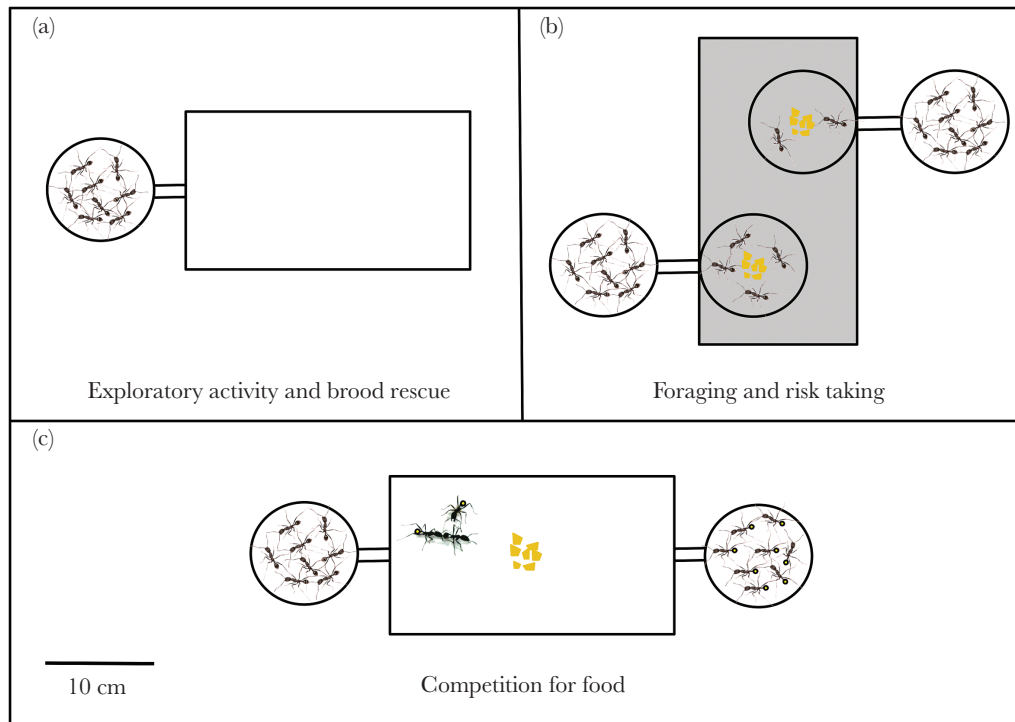
### Colony maintenance and experimental conditions

All experiments were conducted using *A. senilis*, a common ground-dwelling omnivorous species that is widely distributed across the western Mediterranean Basin. In Doñana National Park (southern Spain), *A. senilis* is particularly abundant in xeric sandy areas dominated by open scrublands. Colonies are strictly monogynous (1 queen per colony) and contain between 200 and 3000 workers (Boulay et al. 2007). This species occupies a relatively low rank in the community behavioral dominance hierarchy: it is a subordinate, risk-prone species that forages very close to its critical thermal maximum—the temperature at which locomotor ability is so reduced that individuals can no longer escape lethal temperatures (Cerdá et al. 1998a). However, it is good at discovering and collecting food resources using group recruitment. By using both group recruitment and foraging at high temperatures, *A. senilis* may exploit some food resources better than behaviorally dominant species such as *Tapinoma nigerrimum* and *Lasius grandis* (Cerdá et al. 2009).

We collected colonies in Doñana National Park (Spain) in April 2013. A week after collection, each queen was placed in an artificial nest with 30 workers and all of her colony's pupae. The workers were marked with a small dot of paint (Mitsubishi Pencil UniPaint) on the thorax. They were added to the nests to care for the queen and the pupae, and they were removed 2 weeks after the callows emerged. We thus ended up with 27 colonies, each of which was composed of a queen and workers, which were less than 10 days old. The colonies were placed in artificial nests made of high-quality polystyrene (30 × 15 × 6 cm<sup>3</sup>), kept in a climate chamber (Aralab, Fitoclima 5000) at 25 ± 1 °C and 50% ± 10% relative humidity, given permanent access to water, and fed mealworm (*Tenebrio molitor*) larvae and pieces of butter cookies 3 times a week. Two sets of behavioral trials were conducted, the first when the colonies were 6 weeks old (in June 2013) and the second when the colonies were 17 weeks old (in September 2013).

### Behavioral trials

We created an experimental group of 100 workers and 10 larvae from each colony. We selected only workers that were present in the foraging arena. First, the experimental groups were placed in a Fluon-coated cylindrical container (ø10 × 10 cm<sup>2</sup>) that contained moist cotton for 30 min. Then, each group was subjected to 3 successive trials that aimed to characterize 5 colony-level behavioral traits: boldness, exploratory activity, brood rescue efficiency, foraging activity, and risk taking (Figure 1). All experiments were conducted at room temperature (26 ± 1 °C). Colonies were deprived of food for 72 h before the beginning of the trials. The ants in the experimental groups were returned to their colonies immediately following the last test.



**Figure 1**

Experimental designs of the tests of colony-level personality in *A. senilis*: (a) exploratory and brood rescue behaviors, (b) foraging and risk-taking behaviors, and (c) competition for food resources.

### **Boldness and exploratory activity**

In the first trial, the cylindrical container was connected to a novel environment, a  $27 \times 15 \times 6$  cm<sup>3</sup> arena, via a plastic tube. The group's relative boldness was defined as the mean amount of time spent in the tube by first 8 individuals to enter it. Therefore, colonies that spent less time in the tube were bolder. When a worker returned to the container without entering the arena, she was attributed the maximum recorded time (i.e., 100 s). We then counted the number of ants present in the arena every 30 s for 10 min (each trial was videotaped); the colony's exploratory activity was defined as the mean number of ants present.

### **Brood rescue efficiency**

We measured the time taken by each group to collect 10 pupae that had been placed at the center of the arena (the same one used in the previous test); the trial lasted a maximum of 15 min. We defined brood rescue efficiency as the number of pupae returned to the container divided by the time spent collecting them, from the moment the first pupa was detected.

### **Foraging activity and risk taking**

We connected the first cylindrical container to a second cylindrical container, the arena, whose bottom had been removed. The arena rested on a switched-off electric heating plate (Plactronic Selecta). First, the ants were allowed to explore the arena at room temperature ( $26 \pm 1$  °C); pieces of butter cookie had been deposited in the center. We counted the number of ants present in the arena every minute for 16 min; the group's foraging activity was defined as the mean number of ants present.

We then switched the heating plate on and determined the mean number of ants present in the arena each time the temperature rose by 1° from 46 to 60 °C. The plate took approximately

15 min to reach 60 °C. Forty-six degrees is *A. senilis*' critical thermal maximum, which is defined as the temperature at which workers' locomotor ability is so reduced that they can no longer escape from lethal temperatures (Cerdá et al. 1998a). We thus considered that colonies that were active at temperatures above 46 °C demonstrated collective risk-taking behavior.

### **Behavioral consistency over time**

To assess the consistency of colony behavior over time, we repeated the 3 trials on 17-week-old colonies in September 2013. Only 22 colonies could be tested twice because the others had died or they had lost too many workers or their queen. Hence, overall, 22 colonies were tested for 5 behaviors at 2 different time periods (June and September) (Dingemans and Dochtermann 2013).

### **Colony aggressiveness**

Following the second round of behavioral trials in September, we also assessed colony aggressiveness toward conspecific intruders using the 22 remaining colonies. We did so by introducing 5 alien *A. senilis* workers, one at a time, into each colony for a period of 1 min. The intruders all came from the same colony, which was collected in a different population found in Doñana National Park (Spain). The behavior of the residents toward each intruder was classified as: 1) touch (contacts including prolonged antennation); 2) avoidance; 3) opened mandibles; and 4) fights. We calculated an aggressiveness index for each colony whose value was defined as the mean number of aggressive interactions (categories 3 and 4) divided by the mean number of peaceful interactions (categories 1 and 2).

### **Competition trials**

To test for an association between behavioral types and intra-specific competition, we selected the 6 most proactive colonies

(colonies that were bold, that demonstrated high levels of exploratory activity, and that took greater risks by foraging at high temperatures). Each proactive colony successively faced 2 colonies that were randomly chosen among the 16 remaining colonies. Ants were chilled on ice and marked with a paint spot on the abdomen that reflected colony membership 1 day before the trials started. Two groups of 50 foragers (1 group from each colony) were each placed in a cylindrical container ( $\phi 10 \times 10 \text{ cm}^2$ ) with 10 larvae and moist cotton. The 2 containers were connected to a shared arena ( $27 \times 15 \times 6 \text{ mm}^3$ ) via plastic tubes. After 1 h of acclimation, ants were allowed to enter the foraging arena, which contained 10 pieces of butter cookie in its center (Figure 1). The experiment ended when all 10 cookie pieces had been harvested by the ants. We videotaped the first 20 min of the experiment using a Sony DCR-HC62 camcorder. We counted the number of cookie pieces present in each of the 2 containers. We also recorded the number of aggressive interactions that took place and the number of ants present in the central arena every 2 min for a period of 20 min. We calculated an aggressiveness index for each colony, whose value was defined as the number of aggressive interactions initiated by a given colony divided by the total number of aggressive interactions.

### Statistical analysis

To test for the presence of behavioral syndromes, we analyzed each round of trials (i.e., when colonies were 6 and 17 weeks old) using Principal component analysis (PCA). All the behavioral traits we measured were included in the analysis, but only components with eigenvalues greater than 1 were retained. To study the correlations among the behaviors, we calculated 2-tailed Pearson's correlation coefficients for the pairs of behavioral scores obtained during the different trials. We assessed the consistency of colony behavior across trial rounds using the interclass correlated coefficient (ICC), which is a standard measure of reliability (Bell et al. 2009), and Cronbach's  $\alpha$  index. Finally, we determined whether proactive and reactive colonies differed in competitive ability using a 1-way Anova. These data were  $\log(x + 1)$  transformed prior to conducting the statistical analyses. All statistics were carried out using SPSS 17.0 (SPSS Inc., Chicago, IL).

## RESULTS

### Colony-level syndrome

PCA of 6-week-old colonies revealed a behavioral syndrome described by 2 components that accounted for 54% and 19% of the total variance, respectively, in the 5 behavioral traits (Table 1;

Supplementary data). The first principal component included exploratory activity, foraging activity, and temperature-related foraging risks (negative loading values) as well as boldness (mean amount of time spent in the tube by the first 8 individuals to enter the arena; positive loading value; i.e., colonies with high loading values were shy colonies). The second principal component included brood rescue efficiency (the number of pupae returned to the container divided by the time spent collecting them) (negative loading value).

The Pearson's correlation tests revealed that there were significant relationships among the 4 behaviors forming the first component, which confirms the existence of a complex behavioral syndrome in *A. senilis* (Figure 2, Table 2). This result means that colonies that readily explored novel environments were also bold, demonstrated higher levels of foraging activity, and took more temperature-related foraging risks. In contrast, colonies that less readily explored novel environments were also shyer, demonstrated lower levels of foraging activity, and took fewer temperature-related foraging risks. These 4 correlated behaviors define a proactive-reactive syndrome in *A. senilis* that does not include brood rescue efficiency (correlations:  $P > 0.05$ ).

### Behavioral consistency

The PCA of the 17-week-old colonies revealed the presence of strong structural consistency, defined as consistent temporal correlations among behavioral patterns expressed in 2 or more contexts (Stamps and Groothuis 2010). The composition of the principal components was the same in the second round of trials as in the first (Table 1; Supplementary data). The first and second components explained 49% and 22% of the observed variation, respectively. The first principal component again included exploratory activity, foraging activity, and risk taking (negative loading values) as well as boldness (positive loading value). The second component consisted of brood rescue efficiency (negative loading value).

This structural consistency was partially confirmed by the Pearson's correlations. Correlations among behaviors persisted over time, with the exception of those between boldness and both foraging activity and risk taking (Table 2). As in the first round of trials, brood rescue efficiency was not correlated with the 4 other behaviors composing the proactive-reactive syndrome ( $P > 0.05$ ).

Based on the ICC results, exploratory activity, foraging activity, and risk taking were consistent over a period of at least 11 weeks ( $P < 0.05$ ) (Table 3). Boldness ( $P = 0.06$ ) and brood rescue efficiency ( $P = 0.05$ ) demonstrated marginally insignificant consistency. Cronbach's  $\alpha$  tests produced similar results.

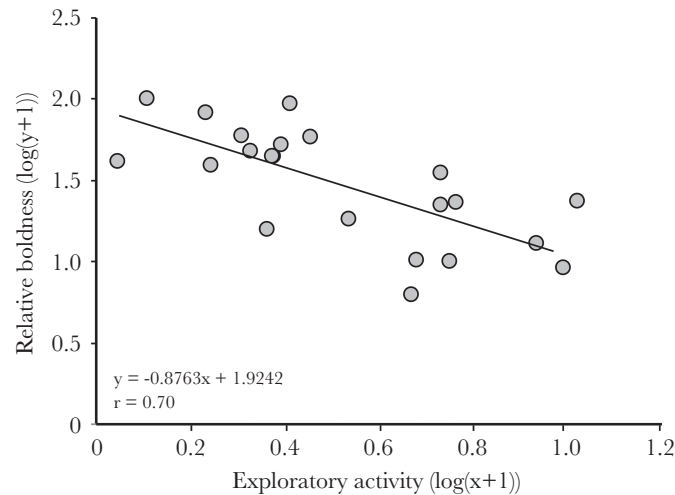
**Table 1**

**Loading values from PCAs of 6-week-old (June) and 17-week-old colonies (September)**

|                      | 6 weeks old  |              | 17 weeks old |             |
|----------------------|--------------|--------------|--------------|-------------|
|                      | PC1          | PC2          | PC1          | PC2         |
| Exploratory activity | <b>-0.88</b> | 0.03         | <b>-0.84</b> | -0.35       |
| Boldness             | <b>0.88</b>  | -0.17        | <b>0.7</b>   | 0.49        |
| Brood rescue         | -0.32        | <b>-0.94</b> | 0.16         | <b>-0.7</b> |
| Foraging             | <b>-0.74</b> | -0.01        | <b>-0.8</b>  | 0.22        |
| Risk taking          | <b>-0.73</b> | 0.17         | <b>-0.75</b> | 0.46        |
| Eigenvalues          | 2.7          | 0.95         | 2.4          | 1.1         |
| % variance explained | 54           | 19           | 49           | 22          |

Significant values ( $>0.7$ ) are shown in bold.





**Figure 2**

Correlation between exploratory activity in a novel environment and boldness in 17-week-old colonies ( $r = -0.70$ ,  $P = 0.006$ ). A colony's relative boldness was determined by averaging the amount of time that it took the first 8 individuals present in the plastic tube to enter the foraging arena.

**Table 2**

**Correlations among behaviors across time (6 weeks of age = shaded; 17 weeks of age = unshaded)**

|                      | Exploratory activity | Boldness     | Brood rescue | Foraging    | Risk taking |
|----------------------|----------------------|--------------|--------------|-------------|-------------|
| Exploratory activity | —                    | <b>-0.70</b> | 0.20         | <b>0.46</b> | <b>0.47</b> |
| Boldness             | <b>-0.80</b>         | —            | -0.08        | -0.34       | -0.15       |
| Brood rescue         | 0.23                 | -0.13        | —            | 0.06        | 0.20        |
| Foraging             | <b>0.47</b>          | <b>-0.43</b> | 0.20         | —           | <b>0.68</b> |
| Risk-taking          | <b>0.41</b>          | <b>-0.49</b> | 0.10         | <b>0.57</b> | —           |

Correlation coefficients for each pair of behaviors are reported in the table. Significant correlations ( $P < 0.05$ ) are in bold.

**Table 3**

**Consistency of colony behavior across time (11 weeks of the experiment)**

|                      | Cronbach's $\alpha$ | ICC         | 95% CI               | $P$         |
|----------------------|---------------------|-------------|----------------------|-------------|
| Exploratory activity | 0.57                | <b>0.37</b> | <b>-0.04 to 0.69</b> | <b>0.04</b> |
| Boldness             | 0.49                | 0.33        | -0.10 to 0.65        | 0.06        |
| Brood rescue         | 0.54                | 0.34        | -0.08 to 0.66        | 0.05        |
| Foraging             | 0.57                | <b>0.40</b> | <b>-0.02 to 0.70</b> | <b>0.03</b> |
| Risk-taking          | 0.64                | <b>0.47</b> | <b>0.07 to 0.74</b>  | <b>0.01</b> |

Consistency was measured using reliability tests, including Cronbach's  $\alpha$  index and ICC. CI were set by an alpha of 0.05 (95% CI). Significant ICC values (indicating consistency) are in bold. CI, confidence intervals.

### Colony aggressiveness

Colony aggressiveness toward intruders was positively correlated with exploratory activity (Figure 3, Pearson's correlation:  $r = 0.51$ ,  $P = 0.02$ ) and negatively correlated with boldness (Pearson's correlation:  $r = -0.49$ ,  $P = 0.03$ ). In other words, the most aggressive colonies were also the boldest and those that most readily explored novel environments. None of the other behaviors were correlated with aggressiveness ( $P > 0.05$ ).

### Competition trials

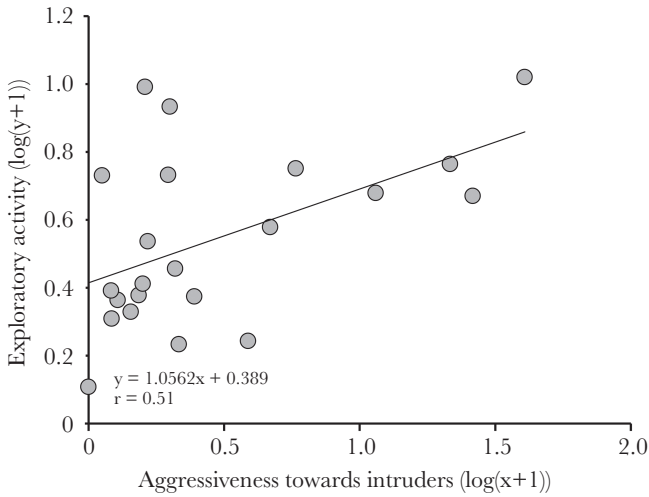
Proactive colonies were more active during the first 20 min of the competition trials (1-way Anova, degrees of freedom [df] = 1,  $F = 11.66$ ,  $P = 0.002$ ) and more efficient at harvesting food resources (8 cookie pieces harvested on average vs. 2 by reactive conspecifics)

(1-way Anova, df = 1,  $F = 36.67$ ,  $P < 0.0001$ ) (Table 4). They were also more aggressive, engaging in more aggressive interactions than reactive colonies (Mann-Whitney  $U$  test,  $P < 0.001$ ,  $n = 12$ ). Furthermore, aggressiveness in the competition trials was positively correlated with aggressiveness in the intruder test (Spearman's correlation,  $r = 0.81$ ,  $P = 0.008$ ) (Figure 4).

## DISCUSSION

### Colony personality and behavioral syndromes

Using colonies of the same age that were kept under standardized laboratory conditions for 11 weeks, we found consistent intercolony variation that persisted over time and across different situations; this variation is the basis for colony personality (Jandt et al. 2014). First, exploratory activity, foraging activity, and risk taking were consistent across time, and boldness and brood rescue efficiency showed the same, if marginally insignificant, trend. Second, *A. senilis* colonies exhibited consistent behavioral differences across different situations. For example, colony aggressiveness in competition trials was positively correlated with colony aggressiveness toward conspecific intruders. The consistent behavioral differences that we observed are in line with those reported in previous studies on aggressiveness (e.g., Modlmeier and Foitzik 2011; Modlmeier et al. 2012) and foraging activity (e.g., Gordon et al. 2011; Wray et al. 2011; Pinter-Wollman, Gordon, et al. 2012) in insects and vertebrates (see Sih et al. 2004). In contrast, exploratory activity has not always been found to remain constant over time. For example, *Temnothorax longispinosus* colonies demonstrated

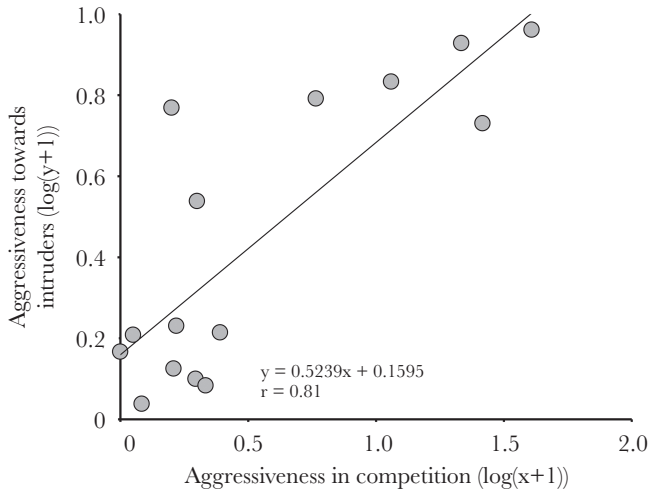


**Figure 3** Correlation between exploratory activity in a novel environment and colony aggressiveness toward conspecific intruders ( $r = 0.51$ ,  $P = 0.02$ ).

**Table 4** Results of the competition trials staged between proactive and reactive colonies

|                | Proactive colonies | Reactive colonies | <i>P</i> |
|----------------|--------------------|-------------------|----------|
| Activity       | 14 ± 1.7           | 8 ± 1.2           | <0.001   |
| Food           | 7.5 ± 0.6          | 2.5 ± 0.6         | <0.001   |
| Aggressiveness | 0.78 ± 0.06        | 0.22 ± 0.06       | <0.001   |

“Activity” refers to the mean number of workers present in the foraging arena, “food” refers to the mean number of food items collected, and “aggressiveness” refers to the mean aggressiveness index of each colony type. All means are ± standard error.



**Figure 4** Correlation between colony aggressiveness in a competitive context and colony aggressiveness toward conspecific intruders ( $r = 0.81$ ,  $P = 0.008$ ).

different levels of exploratory activity at 2 time points separated by 5 months (Modlmeier et al. 2012). Our findings may not concur with those of Modlmeier et al. (2012) because of methodological differences. Modlmeier et al. randomly collected individuals from the entire colony; we only sampled foragers, which probably helped to reduce within-group variability.

Furthermore, the PCAs of the 6- and 17-week-old colonies revealed the existence of a continuum of colony-level behavioral types, related to resource acquisition; colonies ranged from being reactive to being proactive. Proactive colonies were more aggressive, as well as more apt to explore novel environments and take greater risks by foraging at higher temperatures. In contrast, reactive colonies were shyer and less aggressive; they were more cautious when introduced to new environments and took fewer temperature-related risks. This proactive–reactive syndrome (also known as proactive vs. reactive coping) has been described in a wide range of animals, including pigs (Hessing et al. 1993), rodents (Koolhaas et al. 1999), and birds (Pascual and Senar 2014). However, this syndrome remains poorly quantified in ants (Jandt et al. 2014). Modlmeier et al. (2012) observed that in *T. longispinosus*, colonies that displayed more exploratory activity were also more aggressive. In *Myrmica* species, patrollers display an aggressiveness–boldness syndrome, where aggressive workers are also bold when responding to an alarm stimulus (Chapman et al. 2011). We found no correlation between the traits making up this proactive–reactive syndrome and brood rescue efficiency. Contrary to our expectations, proactive colonies did not rescue larvae more rapidly than reactive colonies, likely because brood rescue is performed by a very small subset of specialized workers. For example, in *Temnothorax* species, task distributions are skewed: a few ants carry out most of a given task and many ants carry out a small part of it (Pinter-Wollman, Hubler, et al. 2012).

### Intraspecific competition

Previous studies have linked colony personality and success. In the harvester ant, *Pogonomyrmex barbatus*, colonies were found to differ in their collective responses to changing conditions; their responses were related to variation in the production of offspring colonies (Gordon 2013). Group behavioral type is also related to differences in survival (Pruitt and Goodnight 2014) and collective foraging (Pruitt and Keiser 2014) in social spiders. To our knowledge, this study is the first to link colony behavioral types with specific performance trade-offs: we found that colony personality is directly related to resource competition and temperature-related foraging risks. Proactive *A. senilis* colonies retrieved more food items than their reactive counterparts, probably because they contained more active and more aggressive foragers. Therefore, being bold, active, and aggressive may provide a selective advantage. However, as the existence of behavioral syndromes inherently suggests that behavioral plasticity is limited, such syndromes are often associated with trade-offs (Sih et al. 2004). For instance, we found that proactive *A. senilis* colonies took unnecessary risks by foraging at high temperatures.

*A. senilis* is a relatively thermophilic species that uses group recruitment at temperatures of up to 45 °C when exploiting valuable food resources in the field (Cerdá et al. 1998b); this temperature is very close to its critical thermal maximum (Cerdá et al. 1998a). In the risk-taking trial, proactive colonies continued foraging even at extreme temperatures (of up to 57 °C). These risk-prone colonies may suffer greater mortality by foraging at temperatures above their critical thermal maximum. Therefore, although proactive colonies may outcompete reactive colonies under stable conditions, they may not be able to adequately adjust their behavior in response to changes in temperature. Individuals or groups with different behavioral types often differ in their responses to environmental changes. For example, in fishes, birds, rodents, and ants,

proactive types tend to outperform reactive types under stable environmental conditions, but reactive types outperform proactive types under variable environmental conditions (Coppens et al. 2010; Bengtson and Dornhaus 2014). Studies of rats have shown that shy, docile, and reactive individuals demonstrate more plastic behavior (Koolhaas et al. 1999). In contrast, bold, aggressive, and proactive individuals tend to fail to respond to environmental shifts. The behavioral syndrome we may have identified is thus associated with a trade-off between resource exploitation efficiency and risk of mortality in context-dependent situations. We recognize that our tests of competition and risk taking may not entirely replicate natural conditions. However, regardless of the limitations associated with laboratory studies of animal personality (Niemelä and Dingemans 2014), the proactive–reactive syndrome we detected was probably not the product of the laboratory environment. The fact that workers were born in the laboratory and that behaviors involved in resource acquisition were consistent across time suggests that the syndrome has a genetic basis. In nature, *A. senilis* experiences highly variable environmental conditions; for instance, in the summer, surface temperatures in Doñana may vary from 20 to 70 °C over the course of a few hours. Such variation is probably key in maintaining this proactive–reactive syndrome. However, the next step is to study this trade-off in wild populations of *A. senilis*, by monitoring the daily foraging activity of different colonies and determining their respective levels of fitness. Because this colony-level syndrome is potentially related to the ability of colonies to acquire resources, it is likely that it affects colony fitness. Studying the underlying trade-off will help disentangle why both colony personality types could have been maintained by selection. One would expect that proactive and reactive strategies would persist only if they both conferred equal fitness.

In conclusion, our study demonstrates that a link exists between group behavioral types and specific performance trade-offs in social species. Selection for specific strategies (proactive versus reactive) may depend on both the intensity of competition and environmental conditions. Because proactive colonies are better at resource competition, colonies in dense and/or resource-poor areas should be more proactive (either because of plasticity or natural selection). If there is a genetic basis for proactive behavior, then conditions such as high population density and limited resources could select for traits that make colonies more proactive. Inversely, under harsh conditions and when competition is relaxed, traits that make a colony more reactive could be selected for. Temporal variation in competition and environmental conditions might therefore contribute to the maintenance of colony personality. There is some evidence in the literature that certain specific behavioral traits, such as aggressiveness, exploratory activity, or risk taking, are repeatable and heritable in vertebrates (Dingemans et al. 2002; van Oers et al. 2004); however, examples remain rare in invertebrates (Pruitt et al. 2010; Kralj-Fišer and Schneider 2012). Because social insects can be analyzed at multiple levels (i.e., individuals, castes, and colonies) (Jandt et al. 2014), they are a unique study group, offering exciting new perspectives when it comes to examining ontogeny and the heritability of personality traits (Bengtson and Jandt 2014). Cross-fostering experiments can yield insights on the ontogenetic and hereditary processes that shape phenotypic traits (Purcell and Chapuisat 2012; Keiser, Wright, et al. 2014). By performing cross-experiments, Libbrecht and Keller (2013) have recently demonstrated that both maternal and paternal lineages have effects on behaviors such as foraging and brood care in the invasive ant *Linepithema humile*. Conducting similar experiments with *A. senilis*, a

species with single-mated queens, will help clarify the role played by heritability in behavioral variability among colonies.

## SUPPLEMENTARY MATERIAL

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

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## REFERENCES

- Aplin LM, Farine DR, Mann RP, Sheldon BC. 2014. Individual-level personality influences social foraging and collective behaviour in wild birds. *Proc R Soc Lond B*. 281:20141016.
- Aplin LM, Farine DR, Morand-Ferron J, Cole EF, Cockburn A, Sheldon BC. 2013. Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecol Lett*. 16:1365–1372.
- Bell AM. 2007. Future directions in behavioural syndromes research. *Proc Biol Sci*. 274:755–761.
- Bell AM, Hankison SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis. *Anim Behav*. 77:771–783.
- Bengtson SE, Dornhaus A. 2014. Be meek or be bold? A colony-level behavioural syndrome in ants. *Proc Biol Sci*. 281:20140518.
- Bengtson SE, Jandt JM. 2014. The development of collective personality: the ontogenetic drivers of behavioral variation across groups. *Front Ecol Evol*. 2:1–13.
- Boulay R, Hefetz A, Cerdá X, Devers S, Francke W, Twele R, Lenoir A. 2007. Production of sexuals in a fission-performing ant: dual effects of queen pheromones and colony size. *Behav Ecol Sociobiol*. 61:1531–1541.
- Cerdá X, Angulo E, Boulay R, Lenoir A. 2009. Individual and collective foraging decisions: a field study of worker recruitment in the gypsy ant *Aphaenogaster senilis*. *Behav Ecol Sociobiol*. 63:551–562.
- Cerdá X, Retana J, Cros S. 1998a. Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. *Funct Ecol*. 12:45–55.
- Cerdá X, Retana J, Manzaneda A. 1998b. The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. *Oecologia*. 117:404–412.
- Chang AT, Sih A. 2013. Multilevel selection and effects of keystone hyper-aggressive males on mating success and behavior in stream water striders. *Behav Ecol*. 24:1166–1176.
- Chapman BB, Thain H, Coughlin J, Hughes WOH. 2011. Behavioural syndromes at multiple scales in *Myrmica* ants. *Anim Behav*. 82:391–397.
- Cole EF, Quinn JL. 2014. Shy birds play it safe: personality in captivity predicts risk responsiveness during reproduction in the wild. *Biol Lett*. 10:20140178.
- Coppens CM, de Boer SF, Koolhaas JM. 2010. Coping styles and behavioural flexibility: towards underlying mechanisms. *Philos Trans R Soc Lond B Biol Sci*. 365:4021–4028.
- Dall SRX, Bell AM, Bolnick DI, Ratnieks FLW. 2012. An evolutionary ecology of individual differences. *Ecol Lett*. 15:1189–1198.
- Dall SRX, Houston AI, McNamara JM. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol Lett*. 7:734–739.
- Dingemans NJ, Both C, Drent PJ, Van Oers K, Van Noordwijk AJ. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim Behav*. 64:929–938.

- Dingemans NJ, Dochtermann NA. 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J Anim Ecol.* 82:39–54.
- Dyer JRG, Croft DP, Morrell LJ, Krause J. 2009. Shoal composition determines foraging success in the guppy. *Behav Ecol.* 20:165–171.
- Eldakar OT, Dlugos MJ, Wilcox RS, Wilson DS. 2009. Aggressive mating as a tragedy of the commons in the water strider *Aquarius remigis*. *Behav Ecol Sociobiol.* 64:25–33.
- Eldakar OT, Wilson DS, Dlugos MJ, Pepper JW. 2010. The role of multilevel selection in the evolution of sexual conflict in the water strider *Aquarius remigis*. *Evolution.* 64:3183–3189.
- Gordon D. 1987. Group-level dynamics in harvester ants: young colonies and the role of patrolling. *Anim Behav.* 35:833–843.
- Gordon DM. 2013. The rewards of restraint in the collective regulation of foraging by harvester ant colonies. *Nature.* 498:91–93.
- Gordon DM, Guetz A, Greene MJ, Holmes S. 2011. Colony variation in the collective regulation of foraging by harvester ants. *Behav Ecol.* 22:429–435.
- Gosling SD. 2001. From mice to men: what can we learn about personality from animal research? *Psychol Bull.* 127:45–86.
- Hessing MJC, Hagelso AM, van Beek JAM, Wiepkema RP, Schouten WGP, Krukow R. 1993. Individual behavioural characteristics in pigs. *Appl Anim Behav Sci.* 37:285–295.
- Hui A, Pinter-Wollman N. 2014. Individual variation in exploratory behaviour improves speed and accuracy of collective nest selection by Argentine ants. *Anim Behav.* 93:261–266.
- Jandt JM, Bengtson S, Pinter-Wollman N, Pruitt JN, Raine NE, Dornhaus A, Sih A. 2014. Behavioural syndromes and social insects: personality at multiple levels. *Biol Rev.* 89:48–67.
- Keiser CN, Jones DK, Modlmeier AP, Pruitt JN. 2014. Exploring the effects of individual traits and within-colony variation on task differentiation and collective behavior in a desert social spider. *Behav Ecol Sociobiol.* 68:839–850.
- Keiser CN, Wright CM, Singh N, DeShane JA, Modlmeier AP, Pruitt JN. 2014. Cross-fostering by foreign conspecific queens and slave-making workers influences individual- and colony-level personality. *Behav Ecol Sociobiol.* 69:395–405.
- Keller L. 1999. Levels of selection in evolution. Princeton (NJ): Princeton University Press. p. 272.
- Kleeberg I, Pamminger T, Jongepier E, Papenhagen M, Foitzik S. 2014. Forewarned is forearmed: aggression and information use determine fitness costs of slave raids. *Behav Ecol.* 25:1058–1063.
- Knaden M, Wehner R. 2003. Nest defense and conspecific enemy recognition in the desert ant *Cataglyphis fortis*. *J Insect Behav.* 16:717–730.
- Koolhaas JM, Korte SM, De Boer SF, Van Der Vegt BJ, Van Reenen CG, Hopster H, De Jong IC, Ruis MAW, Blokhuis HJ. 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neurosci Biobehav Rev.* 23:925–935.
- Korb J, Heinze J. 2004. Multilevel selection and social evolution of insect societies. *Naturwissenschaften.* 91:291–304.
- Kralj-Fišer S, Schneider JM. 2012. Individual behavioural consistency and plasticity in an urban spider. *Anim Behav.* 84:197–204.
- Kralj-Fišer S, Schuett W. 2014. Studying personality variation in invertebrates: why bother? *Anim Behav.* 91:41–52.
- Krebs JR, Davies NB. 1997. Behavioural ecology: an evolutionary approach. Oxford: Wiley-Blackwell. p. 464.
- Kurvers RHJM, Prins HHT, van Wieren SE, van Oers K, Nolet BA, Ydenberg RC. 2010. The effect of personality on social foraging: shy barnacle geese scrounge more. *Proc Biol Sci.* 277:601–608.
- Libbrecht R, Keller L. 2013. Genetic compatibility affects division of labor in the Argentine ant *Linepithema humile*. *Evolution.* 67:517–524.
- Modlmeier AP, Foitzik S. 2011. Productivity increases with variation in aggression among group members in *Temnothorax* ants. *Behav Ecol.* 22:1026–1032.
- Modlmeier AP, Keiser CN, Shearer TA, Pruitt JN. 2014. Species-specific influence of group composition on collective behaviors in ants. *Behav Ecol Sociobiol.* 68:1929–1937.
- Modlmeier AP, Keiser CN, Watters JV, Sih A, Pruitt JN. 2014. The keystone individual concept: an ecological and evolutionary overview. *Anim Behav.* 89:53–62.
- Modlmeier AP, Liebmann JE, Foitzik S. 2012. Diverse societies are more productive: a lesson from ants. *Proc Biol Sci.* 279:2142–2150.
- Niemelä PT, Dingemans NJ. 2014. Artificial environments and the study of “adaptive” personalities. *Trends Ecol Evol.* 29:245–247.
- van Oers K, Drent PJ, de Goede P, van Noordwijk AJ. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proc Biol Sci.* 271:65–73.
- Pamminger T, Scharf I, Pennings PS, Foitzik S. 2011. Increased host aggression as an induced defense against slave-making ants. *Behav Ecol.* 22:255–260.
- Pascual J, Senar JC. 2014. Antipredator behavioural compensation of proactive personality trait in male *Eurasian siskins*. *Anim Behav.* 90:297–303.
- Pinter-Wollman N. 2012. Personality in social insects: how does worker personality determine colony personality? *Curr Zool.* 58:579–587.
- Pinter-Wollman N, Gordon DM, Holmes S. 2012. Nest site and weather affect the personality of harvester ant colonies. *Behav Ecol.* 23:1022–1029.
- Pinter-Wollman N, Hubler J, Holley JA, Franks NR, Dornhaus A. 2012. How is activity distributed among and within tasks in *Temnothorax* ants? *Behav Ecol Sociobiol.* 66:1407–1420.
- Pruitt JN, Goodnight CJ. 2014. Site-specific group selection drives locally adapted colony compositions. *Nature.* 514:359–362.
- Pruitt JN, Grinsted L, Settepani V. 2013. Linking levels of personality: personalities of the “average” and “most extreme” group members predict colony-level personality. *Anim Behav.* 86:391–399.
- Pruitt JN, Keiser CN. 2014. The personality types of key catalytic individuals shape colonies’ collective behaviour and success. *Anim Behav.* 93:87–95.
- Pruitt JN, Riechert SE, Iturralde G, Vega M, Fitzpatrick BM, Avilés L. 2010. Population differences in behaviour are explained by shared within-population trait correlations. *J Evol Biol.* 23:748–756.
- Purcell J, Chapuisat M. 2012. The influence of social structure on brood survival and development in a socially polymorphic ant: insights from a cross-fostering experiment. *J Evol Biol.* 25:2288–2297.
- Ruel C, Cerdá X, Boulay R. 2012. Behaviour-mediated group size effect constrains reproductive decisions in a social insect. *Anim Behav.* 84:853–860.
- Scharf I, Modlmeier AP, Fries S, Tirard C, Foitzik S. 2012. Characterizing the collective personality of ant societies: aggressive colonies do not abandon their home. *PLoS One.* 7:1–7.
- Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol.* 19:372–378.
- Sih A, Watters J. 2005. The mix matters: behavioural types and group dynamics in water striders. *Behaviour.* 142:1417–1431.
- Smith BR, Blumstein DT. 2008. Fitness consequences of personality: a meta-analysis. *Behav Ecol.* 19:448–455.
- Stamps J, Groothuis TGG. 2010. The development of animal personality: relevance, concepts and perspectives. *Biol Rev.* 85:301–325.
- Thomas ML, Payne-Makrisà CM, Suarez AV, Tsutsui ND, Holway DA. 2006. When supercolonies collide: territorial aggression in an invasive and unicolonial social insect. *Mol Ecol.* 15:4303–4315.
- Webster MM, Ward AJW. 2011. Personality and social context. *Biol Rev Camb Philos Soc.* 86:759–773.
- Wilson AJ, Grimmer A, Rosenthal GG. 2013. Causes and consequences of contest outcome: aggressiveness, dominance and growth in the sheephead swordtail, *Xiphophorus birchmanni*. *Behav Ecol Sociobiol.* 67:1151–1161.
- Wolf M, Weissing FJ. 2012. Animal personalities: consequences for ecology and evolution. *Trends Ecol Evol.* 27:452–461.
- Wray MK, Mattila HR, Seeley TD. 2011. Collective personalities in honeybee colonies are linked to colony fitness. *Anim Behav.* 81:559–568.
- Wray MK, Seeley TD. 2011. Consistent personality differences in house-hunting behavior but not decision speed in swarms of honey bees (*Apis mellifera*). *Behav Ecol Sociobiol.* 65:2061–2070.