Personality traits are associated with colony productivity in the gypsy ant
***Aphaenogaster senilis*.**

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Abstract

Consistent individual differences in personality traits should be favoured when those traits contribute to consistent individual fitness differences. However, how variations in behaviours are related to productivity remains scarcely explored in social species, particularly in insects. Here, we investigated whether exploratory, boldness and brood rescue behaviours expressed at the colony-level are associated with group productivity that is, colony growth, queen and worker production, and larvae survival in the gypsy ant *Aphaenogaster senilis*. We found that group-level exploratory activity, boldness, and brood rescue efficiency were highly correlated. Furthermore, both exploratory activity and brood rescue efficiency were significantly consistent across 11 weeks. Finally, differences in brood rescue efficiency correlated positively with colony growth, queen and worker production, and larvae survival. These results show that colony-level personality may be linked with differences in colony life-history strategy, which may promote the emergence and maintenance of personality traits in group-living species.

Keywords: animal personality; behavioural syndrome; social insects; life-history productivity.

35 **Significance Statement**

36 When groups of individuals show variation in a series of behaviours that are related to
37 exploratory activity and parental care, is it related to differences in groups' productivity?
38 This is a key question to understand the process underlying the evolution and
39 maintenance of consistent behavioural differences in a population. Here, we
40 investigated whether exploratory, boldness and brood rescue behaviours expressed at
41 the colony-level are associated with group productivity that is, colony growth, queen
42 and worker production, and larvae survival in the gypsy ant *Aphaenogaster senilis*.
43 Overall, this experiment reveals that behaviours in group-living species are linked with
44 group productivity.

45

INTRODUCTION

A major objective of behavioural ecology is to determine the main sources of variation in the expression of animal behaviour (Wolf and McNamara 2012) and to quantify their fitness consequences (Smith and Blumstein 2008). Many studies have shown that, in solitary animals, individuals have correlated behavioural traits (comprising what is known as a behavioural syndrome) and that behavioural differences are consistent across time and context (comprising what is called personality) (Sih et al. 2004). From an ecological and evolutionary perspective, personality traits are important because they can account for apparently maladaptive behaviour in a population (Sih et al. 2004).

Recently, group-living species such as fishes (Dyer et al. 2009), birds (Aplin et al. 2013; Aplin et al. 2014), mice (Schoepf and Schradin 2012), spiders (Pruitt 2012; Holbrook et al. 2014; Pruitt and Keiser 2014; Wright et al. 2015), bees (Wray et al. 2011), and ants (Pinter-Wollman et al. 2012; Hui and Pinter-Wollman 2014; Modlmeier et al. 2014; Cronin 2015; Blight et al. 2016) have been observed to exhibit group-level behavioural syndromes and personality traits. Living in groups is often associated with the specialisation of individuals on different tasks such as offspring care, foraging or group defence (Wright et al. 2014). This task differentiation is hypothesised to enhance the inclusive fitness of group-living individuals by, for instance, reducing predation risk (Roberts 1996; Ale and Brown 2007), or increasing hunting success (Lührs et al. 2013). However whether consistent behavioural differences afford performance advantages for the group remains scarcely explored in group-living species (Webster and Ward 2011). Yet, this seems a key question to understand the process underlying the evolution and maintenance of consistent differences in personality traits in a population. Indeed traits that contribute to consistent differences in productivity should favour consistent individual differences in personality traits (Stamps 2007; Biro and Stamps 2008). Personality traits are often associated with differences in life-history

73 strategies where individuals that focus on future fitness returns should be consistently
74 more risk-averse compared with individuals that have low future expectations (Wolf et
75 al. 2007). This resembles classical r/K selection theory in solitary animals (MacArthur
76 and Wilson 1967). Individuals that place an emphasis on a high growth rate and
77 produce many offspring, each of which has a relatively low probability of surviving,
78 should be relatively risk-prone. Conversely, individuals that reduce the quantity of
79 offspring should be risk-averse. Individuals should therefore adjust their behaviour
80 according to individual life-history strategy, leading to the emergence of personality
81 traits (Wolf et al. 2007). For example, in great tits exploratory behaviour correlated with
82 fitness components for both adult survival and the annual number of recruiting offspring
83 (Dingemanse et al. 2004).

84 Examples from a wide range of solitary species provide evidence for general
85 relationships between personality traits and individual fitness (Smith and Blumstein
86 2008). Conversely, few studies have experimentally addressed this idea in group-living
87 species, despite its ecological and evolutionary implications. This relationship has been
88 recently described in fish, water striders, bees, ants or spiders as presented above. In
89 water striders, group composition has been found to impact overall group mating
90 activity (Eldakar et al. 2009; Chang and Sih 2013). A major factor is the presence of
91 hyper-aggressive males that decrease the group's overall mating activity by driving the
92 females out of the group (Sih and Watters 2005). Variation in behavioural types was
93 also associated with variation in reproductive decisions in a cooperative breeding
94 cichlid (Schürch and Heg 2010). In *Pogonomyrmex* harvester ants, offspring production
95 varies within populations (Ingram et al. 2013): some colonies seem to belong to
96 successful families that produce many offspring, while others produce few to none.
97 Life-history productivity of these colonies is linked with their behavioural tendencies.
98 Colonies that more carefully allocate additional foragers during very hot, physiologically
99 stressful days, produce more offspring (Gordon 2013). In *Temnothorax longispinosus*,

differences in personality traits are linked to differences in *per-capita* productivity (Modlmeier and Foitzik 2011; Modlmeier et al. 2012).

Despite these recent examples, the link between animal personality traits and productivity in group-living species remains under explored. Here we used a variety of relevant fitness components to test for such a relationship in gypsy ants (*Aphaenogaster senilis*). Specifically, we stimulated the production of new queens and recorded larvae survival in queen-less groups. *A. senilis* disperses by colony fission, and most diploid brood develop into workers while only a few develop into queens. However, when the queen dies, several larvae can develop into new queens.(Boulay et al. 2007). After mating, one of these newly produced queens may replace her mother as reproductive in the colony, which is relatively rare in monogynous species. Interestingly, in the absence of the queen, *A. senilis* colonies differ consistently in the number of new queens produced (Ruel et al. 2012; Villalta et al. 2016) which might reflect different strategies, with some colonies investing in the production of several queens (short-term fitness) while others might rather save the cost associated with the production of several queens (long-term fitness). Indeed, queen larvae are approximately 1.5 bigger than worker, requiring probably higher food intake and care from workers. Whether this variation in colony productivity is related to colony behavioural types is unknown.

MATERIAL AND METHODS

Colony maintenance and experimental conditions

In April 2013, we collected 22 colonies that contained large amounts of brood in Doñana National Park (Spain). One week after collection, the queen of each colony was placed in an artificial nest with 30 workers (15 foragers and 15 nurses) and all the pupae. The workers were marked with a small dot of paint (Mitsubishi Pencil UniPaint)

on the thorax and were removed two weeks after the first new workers emergence. We thus obtained 22 colonies composed of a mother queen plus a cohort of 350 to 900 workers, which were all the same age (± 5 days). These colonies were maintained in artificial nests at $25^{\circ}\text{C} \pm 1^{\circ}\text{C}$ and $50\% \pm 10\%$ relative humidity. The artificial nests were connected to a foraging area with permanent access to water. The ants were provided with mealworm (*Tenebrio molitor*) larvae and pieces of biscuits three times a week.

Behavioural trials

When the workers were 6 weeks old, we obtained a test group from each colony composed of 100 workers that were inside the nest and 10 larvae. The test groups were placed in closed Fluon-coated cylindrical containers ($\varnothing 10 \times 10$ cm) where they had access to moist cotton. Blinded methods were not used here. Indeed to prevent observer bias, we choose to videotape each behavioural trial. We did the colonies' behaviour scoring once all the trials were conducted, using only quantitative data that leave no room for observer interpretation (e.g. the number of individuals in an arena every 30s).

Boldness and exploratory activity. Thirty minutes later, the cylindrical containers were connected to a novel arena ($27 \times 15 \times 6$ cm) via a plastic tube ($\varnothing 0.8 \times 5$ cm). First, we estimated colony-level boldness-shyness. This was defined as the mean amount of time spent in the tube by the first 8 individuals to enter it. Therefore, colonies that spent less time in the tube were bolder. The maximum recorded time (i.e., 100 s) was logged for workers that returned to the container without entering the arena. 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. The ants were allowed to calm down in the container for 10 min before we started the brood rescue efficiency test.

Brood rescue efficiency. At the end of the 10 min, the ants were returned to the cylindrical container and we placed 10 pupae in the centre of the arena. We then let the ants re-enter the arena and measured the time they took to return the pupae to the cylindrical container; 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.

The ants in the test groups were returned to their colonies immediately following the brood rescue test. To assess the consistency of colony behaviour over time, we repeated the bioassays when the ants were 17 weeks old. Hence, overall, 22 colonies were tested for 3 behaviours at two different time periods (June and September).

Group-level productivity and larvae survival

We estimated different parameters of group-level productivity and larvae survival.

Colony growth. We counted the number of workers present in each colony at week 6 and week 17. We evaluated colony growth by subtracting the number of workers at week 6 from the number of workers at week 17. To control for a size effect we divided colony growth by the initial size of the colony.

Queen production and larvae survival. We put 200 workers and 30 first-instar larvae from 18 colonies (four had died before the second test at week 22) in plastic boxes (ø10 x 10 cm) immediately after field collection and again at week 22. The plastic boxes were connected to a glass tube containing water. In this experiment we evaluated larvae survival and the production of new queens. We monitored larval development (production of workers, queens, and males) for six weeks. The ants were fed mealworms three times a week.

Data analysis

We tested for relationships among behaviours using nonparametric Spearman's rank

correlations. We assessed the consistency of colony behaviour between week 6 and week 17 using the interclass correlation coefficient (ICC), which is a standard measure of repeatability (Bell et al. 2009). General linear mixed models (GLMMs) were fitted to test the relationships between measures of colony productivity (colony growth, larvae survival, female production, and queen production) and behaviours (exploratory activity, boldness-shyness, and brood rescue efficiency). Colony identity and trials were included as a random effect. GLMMs were fitted using Poisson or quasi-Poisson distributions depending on over-dispersion. All statistics were carried out using R (R Core Team; packages ICC 2.2.1, Hmisc 3.14.6, and lme4 1.1.7).

Results

Group-level syndrome

The 18 colonies differed in their levels of boldness, exploration activity and brood rescue efficiency. The Spearman correlation rank tests revealed significant relationships among the three behaviours at week 6 and week 17, suggesting the existence of a complex behavioural syndrome in *A. senilis* ($p < 0.05$) (Table 1). This result means that colonies that readily explored novel environments were also bold, and more efficient at brood rescue. In contrast, colonies that less readily explored novel environments were also shyer, and less efficient at brood rescue. The most active colony sent out in maximum 20 workers during the exploration test against two workers for the least active colonies. The high strength of the correlation recorded between exploratory activity and boldness might be a result of non-independent measurements. Based on the ICC results, exploratory activity and brood rescue efficiency were consistent between the two sets of trials separated by 11 weeks ($p < 0.05$) (Table 2). In contrast the boldness-shyness behaviour was not consistent over time ($p = 0.42$).

Group-level productivity and larval survival

Colony growth was positively associated with both brood rescue efficiency ($t=3.2$, $p<0.01$, Fig. 1) and boldness-shyness ($t=2.15$, $p<0.05$) but was independent of exploratory activity ($t=1.42$, $p>0.05$) (Table 3). The brood rescue behaviour was also positively related to larvae survival ($z=2.16$, $P<0.05$), female production (worker + queen) ($z=2.04$, $p<0.05$) and queen production ($z=2.35$, $p<0.05$) (Table 3). In contrast these three components of colony fitness were independent of both exploratory activity and boldness-shyness ($p>0.05$) (Table 3).

Discussion

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 (Table 2). These results support the notion that *A. senilis* exhibits colony-level personality (Blight et al. 2016). Furthermore the three behavioural variables measured were correlated within colonies at both 6 and 17 weeks (Table 1). Hence, the colonies that most readily entered the new arena were also the most active and most efficient at rescuing pupae. Overall, these results concur with those of recent studies showing the existence of consistent behavioural differences among colonies and colony-level behavioural syndromes (Bengston and Dornhaus 2014; Jandt et al. 2014; Cronin 2015; Blight et al. 2016).

What are the consequences of colony-level behavioural syndromes for colony productivity? Differences in brood rescue efficiency were associated with differences in productivity: we found a significant positive relationship between brood rescue behaviour and total larvae production, female production, and more specifically, queen production. More efficient brood rescue behaviour was also associated with higher colony growth (Figure 1, Table 3). Finally, colony boldness was positively associated with colony growth, but exploratory behaviour was not related to any aspect of productivity measured here. These results clearly show that colony behavioural type is linked with the production and survival of both workers and queens and may therefore

ultimately affect colony fitness. Colonies that were more efficient at brood rescue may also be composed of workers that spend more time caring for larvae and that provide them with more/richer food, thus increasing their survival rate and the probability that they will develop into queens. This agrees with a recent study that demonstrated the joint role of workers and early determination in the development of larvae into queens in *A. senilis* (Villalta et al. 2016).

We demonstrated that colonies of *A. senilis* consistently differ in their productivity (growth and queen production), and that such productivity is correlated to colony behavioural type. This result suggests that evolutionary mechanisms maintaining variation in personality traits in a population are mediated by life-history trade-offs where colony behaviour consistently varies according to life-history strategies (Stamps 2007; Wolf et al. 2007; Biro and Stamps 2008). Life-history theory predicts that bold individuals invest in short-term fitness while shy individuals invest in long-term fitness, and this variation in boldness is maintained due to a “trade-off” in fitness consequences (e.g. growth and mortality, fecundity and mortality or fecundity and survival). Therefore, the behavioural type of an individual or a group should be matched to the life-history strategy of the individual or the group, while variation in life-history strategy may be dependent upon environmental conditions such as extreme temperatures or competition. This has been observed in the social spider *Anelosimus studiosus*, where colonies founded by docile individuals grow more rapidly in size, produce more offspring colonies per year but suffered reduced longevity (Pruitt 2012). In great tits, fast-exploring individuals seem to better defend and obtain a high quality territory, while slow-exploring individuals seem to be better parents (Both et al. 2005). In harvester ant (*Pogonomyrmex barbatus*), variation among colonies in collective response to changing conditions is related to variation in the production of offspring colonies (Gordon 2013). More successful colonies tend to forage less when conditions are harsh, and show relatively stable foraging activity under stable environmental conditions.

According to life-history theory, risk-prone colonies of *A. senilis* that are the most efficient at brood rescue, produce more queens and have a higher colony growth, should invest in short-term fitness, while risk-averse colonies that have a slower growth and produce fewer queens should invest in long-term fitness. To quickly produce a high number of queens and workers, workers need to take risks, such as foraging in harsh conditions (e.g. extreme temperatures) to exploit resources and allocate more energy towards larvae. Risky behaviour may ultimately decrease their longevity. Conversely, colonies that have a slow growth and produce less queens, do not need a constant high food intake which in turn decreases risk-taking and may increase worker longevity. We recently demonstrated that colonies of *A. senilis* differ consistently in behaviours related to food intake, i.e. foraging activity and risk-taking (Blight et al. 2016). Risk-prone colonies that are the most active during foraging, are the most efficient during competition tests for food resources. In return, they suffer more deaths by foraging above their critical thermal maximum (Blight et al. 2016). However more research is necessary, such as information on longevity of colonies of both life-history strategies to confirm this hypothesis.

Our tests of personality and productivity may not entirely replicate natural conditions. In the wild, both the production and survival of workers and queens depend not only on brood care behaviours but also on other behavioural traits such as foraging-related risk-taking or the ability to modulate foraging based on resource distribution and abundance, and environmental conditions (Cerdá et al. 2009), factors that we controlled for. In acorn ants (*Temnothorax longispinosus*), colony productivity in the laboratory depends on intracolony behavioral variations in brood care and exploration (Modlmeier and Foitzik 2011), whereas in the field it depends on intracolony variance in aggression (Modlmeier et al. 2012). Regardless of the limitations of animal personality study in the laboratory (Niemelä and Dingemanse 2014), the relationship between colony behavioural type and life-history productivity we detected was strong enough to be monitored in a laboratory environment. The fact

that workers were born in the laboratory and that activity and brood rescue behaviour were consistent across time suggests that the syndrome has a genetic basis. There is some evidence in the literature that certain specific behavioral traits, such as aggressiveness, exploratory activity, or risk taking, are consistent and heritable in vertebrates (Dingemanse et al. 2002; van Oers et al. 2004); however, examples remain rare in invertebrates (Pruitt et al. 2010; Kralj-Fišer and Schneider 2012). Brood care seems to be heritable and independent of prior experience in ants (Muscedere et al. 2013), suggesting that behavioural ability and/or propensity may be affected by the individual genotype (Oldroyd and Fewell 2007; Waddington et al. 2010; Constant et al. 2012; Wright et al. 2014).

To conclude, a pace-of-life syndrome (sensu Réale et al. 2010) at the colony level may occur here where two strategies (low productivity long-lived colonies vs. high productivity short-lived colonies) could have equivalent lifetime fitness. We demonstrate using an ant species that personality traits and behavioural syndrome in group-living species are linked with group life-history strategy, just as in solitary animals. This supports the life-history theory proposed to explain the emergence and maintenance of consistent behavioural differences in a population. Future research should investigate the association between personality traits and costs of differential life-history strategies to maximise short- or long-term fitness in group-living species.

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457 Figure 1 Relationship between mean brood rescue (number of pupae returned to the
458 nest divided by time at week 6 and week 17) and colonies' growth (subtraction of the
459 number of workers at week 6 from the number of workers at week 17) weighted by
460 initial colony size.

461

462

Table 1 Spearman rank test correlation coefficients for each pair of behaviours (6 weeks of age=shaded; 17 weeks of age=unshaded).

	Exploration	Boldness-shyness	Brood rescue
Exploration	-	-0.70 ; p<0.001	0.49 ; p=0.02
Boldness-shyness	-0.95 ; p<0.001	-	-0.50 ; p=0.018
Brood rescue	0.52 ; p=0.013	-0.59 ; p=0.04	-

Table 2 Consistency of colony behaviour across the 11 weeks of the experiment expressed as the intraclass correlation coefficient (ICC) and its 95% confidence interval (CI). Significant values (indicating consistency) are in bold.

	ICC	95% CI	<i>P</i>
Exploratory activity	0.46	0.06 to 0.73	0.013
Boldness-shyness	0.007	-0.41 to 0.42	0.419
Brood rescue	0.35	-0.07 to 0.67	0.0496

Table 3 Results of GLMM fitted to test the relationship between components of colony productivity (colony growth, larvae survival, females production (worker + queen), queen production) and the behavioural traits.

	<i>df</i>	Colony growth		Larvae survival		Female production		Queen production	
		<i>t</i>	<i>p</i>	<i>z</i>	<i>p</i>	<i>z</i>	<i>p</i>	<i>z</i>	<i>p</i>
Exploratory activity	35	1.42	0.17	-0.73	0.46	0.32	0.78	-1.1	0.27
Boldness-shyness	35	2.15	0.04	1.17	0.24	1.56	0.12	0.16	0.87
Brood rescue	35	3.2	0.003	3.44	0.0006	3.11	0.002	2.35	0.02

Figure 1