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Abstract

The link between individual and group-level behaviour may help understanding cooperation and division of labour in social animals. Despite the recent surge of studies, especially in social insects, the way individual differences translate into group performance remains debated. One hypothesis is that groups may simply differ in the average personality of their members and this would translate into inter-group differences in collective behaviour. We tested the hypothesis of a linear relationship between individual and group phenotype in the ant Formica fusca by using same-age groups of workers after measuring an individual behavioural trait. Individual exploratory activity in an open-field arena was significantly repeatable. Based on this trait, groups were composed, each consisting of 6 individuals with similar exploration tendency housed with 3 cocoons and a refuge. Individual exploratory activity was associated with the performance in cocoon recovery at the group level: groups composed of high exploratory individuals started transporting displaced cocoons significantly earlier and transported more cocoons into the refuge than groups with low exploratory workers. When in a group, more exploratory animals showed significantly more returns to the refuge than less exploratory ones and tended to transport more cocoons. These results show a direct linear link between individual and collective behaviour, suggesting that colony personality reflects the average personality of workers involved in a given task.

Keywords	Social insects; Behavioural type; Collective behaviour; Exploration; Conformity

Corresponding Author	Claudio Carere
Corresponding Author's Institution	University of Tuscia
Order of Authors	Claudio Carere, Celine Audebrand, Heiko Rödel, Patrizia d'Ettorre

Suggested reviewers	Giovanni Polverino, Isaac Planas-Sitja, Wiebke Schuett, Charlotte Hemelrijk, Jonathan Pruitt

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Professor Johan J. Bolhuis
Editor Behavioural Processes

Paris, July 11th 2018

Object: Cover letter ms BEPROC_2018_36 R2

Dear Editor:

Thank you for your letter dated July 10th 2018 concerning the acceptance of our article "Individual behavioural type and group performance in *Formica fusca* ants" pending minor revisions

We have now revised our manuscript and incorporated all the final comments/suggestions of the reviewer (in red).

Looking forward to hearing from you

On behalf of my co-authors

Sincerely

Claudio Carere

-Reviewer 2

In this version of the manuscript authors have improved the methodological details, which helps to better understand how they performed the study. In addition, they have modified the results and discussion section to better focus on the relationship between the average individual behaviour and group-level behaviour. The manuscript in its current version is clearer and focuses on a relevant and timely topic, in agreement with the scope of the journal. I just have some minor points here below.

AU: We thank the reviewer for the positive appreciation of our work and the time taken to read and comment on it

Minor comments:

l 162: I suggest "each originating from one of the 3 sub-colonies". If I understood it well, each group originated from one sub-colony. The current phrasing seems to imply that each group was composed from ants coming from the 3 different sub-colonies.

AU: changed as suggested (L 162-163)

l 192: Delete "linear-mixed effects models". LMM have been defined in line 187, no need to give definition again.

AU: deleted

l 294-303: In this part of the paragraph, authors give some examples in fish, then some perspectives about their study and come back to fish again. It would be better if authors gave all the examples in fish and finished the paragraph with the perspective of studying group size in ants. This could be simply done by just moving two sentences. For instance, I suggest to start in line 294 (after reference 'Brown and Irving, 2014') with "A recent study on stickleback […] (Jolles et al 2017)", as it is still an example about fish and the link between individual and group behaviour. Afterwards, authors could follow by "Finally, a study manipulating group composition in mosquitofish […] (Cote et al 2011)". This way introducing here the idea of group-size, which leads to an ending sentence related to their study and perspectives: "In our study, group size was kept constant and it would be interesting to test the possible influence of group-size [...]".

AU: we agree and moved the sentences as suggested (L 294-301)

l317: The connection between these two sentences is a little awkward. In fact, cooperative prey retrieval and the formation of subgroups during foraging is very common in ants. Nevertheless, it looks like this behaviour and the example given is limited to polydomous species. A sentence introducing foraging behaviour in ants is needed, before giving the example. I suggest something like: "[…] isolated nest chambers. In addition, most ant species form subgroups of individuals during their normal activities (e.g., foraging and prey

retrieval). An interesting example comes from […] (Robson & Traniello, 2002). We show here that, if homogeneous, the performance of these groups directly reflect the average […]"

AU: thank you, we have inserted the suggested sentence L 317-319

- Groups of ant workers with homogeneous personality composition were formed
- Group performance in cocoon retrieval was scored
- Within group differences held consistently across two tasks
- Individual personality persisted in the group context
- Average individual personality prevailed in the group performance

Individual behavioural type and group performance in *Formica fusca* ants

Claudio Carere[1,2]*, Celine Audebrand[1], Heiko G. Rödel[1], Patrizia d'Ettorre[1]

[1] *Laboratoire d'Ethologie Expérimentale et Comparée EA4443, Sorbonne Paris Cité, France*

[2] *Department of Ecological and Biological Sciences, University of Tuscia, Italy*

Short title: Individual and group behaviour in ants

***Corresponding author:** claudiocarere@unitus.it tel. +39 334 3287002

ABSTRACT

The link between individual and group-level behaviour may help understanding cooperation and division of labour in social animals. Despite the recent surge of studies, especially in social insects, the way individual differences translate into group performance remains debated. One hypothesis is that groups may simply differ in the average personality of their members and this would translate into inter-group differences in collective behaviour. We tested the hypothesis of a linear relationship between individual and group phenotype in the ant *Formica fusca* by using same-age groups of workers after measuring an individual behavioural trait. Individual exploratory activity in an open-field arena was significantly repeatable. Based on this trait, groups were composed, each consisting of 6 individuals with similar exploration tendency housed with 3 cocoons and a refuge. Individual exploratory activity was associated with the performance in cocoon recovery at the group level: groups composed of high exploratory individuals started transporting displaced cocoons significantly earlier and transported more cocoons into the refuge than groups with low exploratory workers. When in a group, more exploratory animals showed significantly more returns to the refuge than less exploratory ones and tended to transport more cocoons. These results show a direct linear link between individual and collective behaviour, suggesting that colony personality reflects the average personality of workers involved in a given task.

*Keywords***:** Social insects; Behavioural type; Collective behaviour; Exploration; Conformity

1. Introduction

Grouping behaviour is ubiquitous in the animal kingdom (Krause and Ruxton, 2002). A major question is how individual variation shapes group characteristics. This is crucial because group composition can affect both individual and group fitness (e.g., Mattila and Seeley, 2007; Pruitt, 2012). Despite individual variability may enhance group performance, in some cases group members need to adjust their behaviour to conform to the majority (conformity effect, Day et al., 2001; Brown and Laland, 2002). However, losing individuality might be detrimental to the group and might result in collective errors (Herbert-Read et al., 2013). There is evidence that the benefits, success, and performance of a cohesive group are greater when individuals behave similarly within and across tasks, especially in collective behaviours requiring coordination and motion such us schooling and flocking. Indeed, theoretical models of collective behaviour often assume that group members are equal in their movements and responsiveness to neighbours and other stimuli (Couzin et al., 2005; Sumpter, 2010; but see Romey, 1996). However, in some cases, social context may enhance behavioural differentiation among individuals due to social selection (Jolles et al., 2017). Assumptions of homogeneity and conformity contrast with increasing documentations of consistent inter-individual differences in behaviour, even within groups (Planas-Sitjà et al., 2015; Jolles et al., 2017), implying that group members may be able to buffer or limit (some of) their individual distinctiveness to achieve effective group performance and cohesion, as shown in fish shoals (Herbert-Read et al., 2013). In the past decade, many studies on insects and spiders showed that behaviourally diverse groups outperform monotypic groups in many kinds of tasks because of the presence of experienced individuals and/or genetically different individuals enhancing division of labour (Nonacs and Kapheim,

2007; Langridge et al., 2008; Pruitt and Riechert, 2011; Modlmeier et al., 2012; Hui and Pinter-Wollman, 2014). For instance, in *Temnothorax* ants, intra-colonial behavioural variability increased colony productivity, suggesting a selective advantage of such variation (Modlmeier and Foitzik, 2011).

In non-human animals, including social insects, personality differences, i.e. consistent individual variation in clusters of behaviours across time and/or contexts, have become a major realization underlying many evolutionary and ecological processes and are often predictors of fitness outcomes and life-history traits (e.g., Wolf and Weissing, 2012; Carere and Maestripieri, 2013; Jandt et al., 2013). There are now cogent theoretical arguments and growing empirical evidence to predict that personality differences should translate into difference at the group level and influence social processes and the functioning of animal groups (Webster and Ward, 2011; Jandt et al., 2013; Pruitt et al., 2013; LeBoeuf and Grozinger, 2014; Wolf and Krause, 2014; Cronin, 2015). Several mechanisms explaining how such a link between individual differences and group performance could emerge have been discussed (Wolf and Krause, 2014), including the disproportionate effect of so-called "keystone individuals" demonstrated in social spiders (Modlmeier et al., 2014; Pruitt and Keiser, 2014), and other species (e.g. water striders, Sih and Watters, 2005; zebrafish, Vital and Martins, 2011). In cockroaches (*Periplaneta americana*), stable between-group differences in sheltering behaviour were observed, which derived from the individual personality and social amplification, favouring similar behaviours within a group and contributing to increase differentiation between groups (Planas-Sitjà et al., 2015).

Social insect colonies contain groups of individuals performing different tasks, such as nursing, foraging, and nest maintenance, and natural selection is expected to act

on variation among colonies (Keller, 1999). Until a few years ago, inter-individual behavioural variation in social insects, given also their typical within-colony genetic relatedness, was assumed to be of minor relevance. However, there is now compelling evidence that they harbour relevant personality-related variability at the colony, but also at the caste and individual level (Chapman et al., 2011; Wray et al., 2011; Bengston and Dornhaus, 2014; Kühbandner et al., 2014; Blight et al., 2016; Udino et al., 2016; d'Ettorre et al., 2017). This, in turn, raises questions about the adaptive value of a mix *versus* homogeneity of personality types within colonies (Pinter-Wollman, 2012; Jeanson and Weidenmüller, 2014).

Based on the assumption that, as in social groups of other taxa, "colony personality in eusocial insects emerges from the aggregation of the personality of the workers that comprise it", Pinter-Wollmann (2012) outlined three hypotheses explaining how consistent individual differences of workers may lead to consistent differences at the group level: (*i*) groups differ in average personality of their workers; (*ii*) the distribution rather than the average varies consistently among groups; (*iii*) group level personality does not emerge from individuals, but from other external factors. Note that this author refers to worker personality as a "…measure of how a worker performs any task. For example, an active worker might perform much of any task, whereas an inactive worker might perform very little of any task". In the present study we tested Pinter-Wollman's hypothesis (*i*) by constructing homogenous groups of workers of known age and behavioural type, assessing their performance as a whole, and recording the individual behaviour during the group performance.

We used captive colonies of *Formica fusca* ants, a species that is broadly distributed, to first characterize individuals for a widely used personality trait,

114 exploratory activity in an open-field (which has been characterized also in carpenter
115 ants, *Camponotus aethiops*: Udino et al., 2016; d'Ettorre et al., 2017) including the
116 establishment of its repeatability over time. Then, we formed three types of groups with
117 different average composition but same group size: high-exploratory workers, low-
118 exploratory workers and intermediate workers. Workers of all groups had the same age.
119 The behaviour of the same individuals was scored both when performing alone and
120 when acting in the group. We posed two questions: (i) is group behaviour explained by
121 the features of the individuals forming the group? (ii) are individual differences
122 persistent when behaving in a group? Individual variation can affect group phenotype in
123 a linear or non-linear manner. In the first case, the group behaviour is an average of the
124 individual behaviour of its components; alternatively, the group outcome may reflect
125 the behaviour of the most extreme individuals (LeBoeuf and Grozinger, 2014). If social
126 insects groups are characterized by a linear relationship between individual and group
127 phenotype, we expect that group behaviour would be linearly explained by the average
128 personality of its members and individual differences should persist. We designed our
129 experiments to test whether average behavioural type dominates in a group
130 performance.
131

132 **2. Material and Methods**

133 *2.1 Study animals and formation of same-age groups of workers*

134 Three queenright colonies of *F. fusca* were collected near Rambouillet (Île de France)
135 and maintained in laboratory conditions (25°C ± 2, light-dark cycle 12:12, 50%
136 humidity). Ants were fed with a honey-apple mixture and mealworms and water was
137 provided *ad libitum*. From these source colonies, we formed 3 sub-colonies (1 per

source colony) constituted by about 30 workers marked with a dot of enamel paint (uniPAINT©) on the gaster. Colonies were placed in a plastic box (Ø 8 cm) with plaster floor and kept in the dark (nest) connected with plastic hose to another box (Ø 12 cm) exposed to light (foraging area). The boxes were coated with polytetrafluoroethylene to prevent ants from escaping. We then added 20-30 cocoons at an advanced stage of development to each of the sub-colony. About a week later, the new workers eclosed from the cocoons and could be recognized by the absence of the colour dot. We thus had groups of young workers of very similar age, therefore removing a potential confound for the experimental group composition. These ants having the same age were individually marked and used for the single-cohort experiment described below when they were about two months old.

2.2 Exploratory activity test of individual ants and constitution of homogeneous groups

The exploratory activity of each individually marked ant was evaluated in a circular open-field arena (Ø 11.5 cm) away from the nest (Udino et al. 2016) with a floor of clean filter paper, which was renewed after each trial. The ant was introduced into an acclimatization tube (Ø 3 cm) for 120 s. Then, the tube was removed and the time spent exploring (time of mobility) was measured for 300 s. The ant was then returned to her sub-colony and tested one week later in the open-field arena to check for repeatability.

The sum of the time spent moving during the first and the second open-field test was calculated for each individual and the ants were ranked from the less exploratory to the most exploratory within each sub-colony. We could test 18 individuals per sub-colony and therefore we formed 3 groups of 6 individuals each, with one group made of the 6 least exploratory individuals, one group made of the 6 most exploratory

individuals and one group made of the intermediate individuals, each originating from one of the 3 sub-colonies. Therefore, in total we had 9 groups composed by 6 individual each originating from 3 sub-colonies ($N_{individuals}$ = 54). Each group was placed in a plastic box (Ø 8 cm) exposed to the light and containing a darkened small plastic tube (Eppendorf, 1.5 ml) with a piece of humid cotton at the bottom serving as refuge (nest), and each group was provided with 3 cocoons placed in the box at about 1 cm from the nest entrance. The ants were given honey diluted in water as food and left two days to acclimatize; during this period they transported the cocoons into the nest.

2.3 Disturbance test at the group level

The small plastic tube serving as nest was lifted by the experimenter, turned upside down with the opening towards the floor of the box and hit three times so that all the ants and the cocoons drop in the box. Then, the nest tube was replaced in the box and the number of cocoons as well as the latency time to bring the cocoons back to the nest was recorded during 15 min. The number of individuals returning to the nest and their latency were also recorded. This disturbance may have caused a mild stress to the ants but this would hardly have masked individual differences, since individual differences in response to stress are linked to personality traits and may become even more apparent upon stressful challenges (Carere et al., 2010, Rangassamy et al., 2016). The test was repeated once after one week.

2.4 Statistical analysis

All statistical analyses were done with R, version 3.3.0 (R Core Team 2016). We checked for individual-based repeatability (R_{ICC}) across trials in the animals' exploratory tendency (response variable) by intra-class correlation, calculated as the proportion of phenotypic variation that can be attributed to between-subject variation (Lessells and Boag, 1987). This was done by linear mixed-effects models (LMM) implemented in the R package *rptR* (Nakagawa and Schielzeth, 2011), using individual identity as a random factor. Colony identity was included as further random factors to adjust for potentially confounding effects of the animals' colony origin. *P*-values were calculated by 1000 permutations.

Associations across context at the group level (N = 9) were tested by LMM based on restricted maximum likelihood estimates by using the *lme* function of the R package *nlme* (Pinheiro et al., 2016), including colony identity and group identity as random factors (random effects of group identity nested within colony identity). To test for associations at the individual level (N = 54) between the animals' exploratory activity (time spent in locomotor activity, averaged over the 2 test trials) and the cocoons transported (count variable with 3 levels: 0 cocoons transported during two trials; cocoons transported during 1 trial; cocoons transported during 2 trials) as well as the number of returns to the nest (count variable with 3 levels: 0 returns; returning during 1 trial; returning during 2 trials) we also applied LMM using the *lme* function, including colony and group identity as random factors. *P*-values for LMM were calculated by Monte Carlo sampling with 1000 permutations, using the *PermTest* function of the R package *pgirmess* (Giraudoux, 2016). Permutation tests for linear models are well adjusted for moderate sample sizes and do not require normal

distribution of model residuals (Good, 2005). However, we verified homogeneity of variances for all models by plotting residuals versus fitted values (Faraway, 2006).

For all significant covariate effects of LMM, we provide the slopes (β; based on scaled values) including their standard errors as a measure of (standardized) effects size. Furthermore, we calculated Nagelkerke's Pseudo R^2 based on maximum likelihoods, which can be interpreted as a measure of explained variation (Nagelkerke, 1991).

3. Results

3.1 Consistent individual differences in exploration

On average, *F. fusca* ants explored the test arena during 45.1% of the time of testing (min: 0%, max: 99.3%, average of the two trials). This exploratory activity was significantly repeatable at the individual level across both test trials (LMM-based intra-class correlation with permutations: $R_{ICC} = 0.513$, $N_{individuals} = 54$, $p < 0.001$).

3.2 Differences at the group-level behaviour and contribution of individuals

Groups formed by individuals with higher exploratory activity transported significantly more cocoons into the nest (LMM with permutations: $\beta = 0.798 \pm 0.185$ SE, ${}_{Pseudo}R^2 = 0.676$, $N_{groups} = 9$, $p = 0.004$; Fig. 1a). In addition, such groups showed a significantly lower latency until the first cocoon was transported into the nest ($\beta = -0.906 \pm 0.149$ SE, ${}_{Pseudo}R^2 = 0.824$, $N_{groups} = 9$, $p = 0.001$; Fig. 1b). At the individual level ($N = 54$), during the group task there was a statistical tendency of a positive association between the animals' exploratory activity and the occurrence of cocoon transport events during the two different trials ($\beta = 0.251 \pm 0.135$ SE, ${}_{Pseudo}R^2 = 0.094$, $p = 0.055$).

Furthermore, in groups composed by individuals with higher exploratory activity, a significantly higher percentage of individuals entered the nest within 15 minutes of testing (LMM with permutations: $N_{groups} = 9$, $\beta = 0.699 \pm 0.110$ SE, $_{Pseudo}R^2 = 0.774$, $P < 0.001$; Fig. 2a). There was no significant association between the average exploration tendency of the group and the latency until the first individual entered the nest (LMM with permutations: $\beta = -0.529 \pm 0.317$ SE, $_{Pseudo}R^2 = 0.279$, $P = 0.184$). However, at the individual level ($N = 54$) and including group identity as random factor, there was a significant and positive association between the individuals' exploratory tendency and the occurrence of returns to the nest during the two different trials ($\beta = 0.438 \pm 0.123$ SE, $_{Pseudo}R^2 = 0.125$, $P < 0.001$). Ants that returned to the nest during both trials showed a higher exploratory activity during the open field test than ants that did not enter the nest during any of the trials (Fig. 2b).

4. Discussion

We used *Formica fusca* workers to test whether ant groups are characterized by a linear relationship between individual and group phenotype in laboratory experiments. Our study first showed individual behavioural consistency across time in ant workers when tested individually for exploratory activity. More specifically, we formed a "gradient" of groups composed of individuals with increasing average exploratory tendencies. After an experimental disturbance, groups formed by more exploratory individuals were faster in initiating brood retrieval and retrieved more cocoons overall than groups formed by less exploratory individuals. Also, in the more exploratory groups, a higher proportion of individuals entered the nest than in groups composed by less exploratory workers. During the group task, more exploratory workers showed a significantly higher

return probability to the nest, most probably due to their higher distance covered per time unit. Such individuals also tended to retrieve cocoons with a higher probability than workers that were less exploratory during the individual test. Although we did not explicitly test for the possible effects of the presence of individuals with extreme personalities and the homogeneity of personalities within groups, the present results indicate that the group's behaviour reflects the average behaviour of its members. In other words, these results suggest a linear association between individual and group-level characteristics, in which synergistic effects are not apparent (Pinter-Wollmann, 2012; LeBoeuf and Grozinger, 2014).

Several studies investigated the phenotype of social groups taking into account the behavioural type of the individuals composing them. In general, there is evidence that certain group performances are driven by the average behaviour of the group members. In honeybees *Apis mellifera*, a positive correlation was found between the number of infected larvae removed from the nest and the number of hygienic bees in the group (Paleolog, 2009). Similarly, in *Rhytidoponera confusa* ants, the number of aggressive individuals relates positively to overall colony aggressiveness (Crosland, 1990). In *Bombus terrestris,* the learning performance of individual bees is correlated with the foraging performance at the colony level under natural conditions (Raine and Chittka, 2008). However, these studies did not provide evidence that individual behavioural phenotypes were stable over time (i.e. repeatability) both when alone and in the social context, as would be required to refer to them as a personality trait. Nor did these studies demonstrate a correspondence between individual-level assays conducted in isolation and the behaviour of the same individuals in a social context. Our study includes an assessment of the consistency over time of individual and group behaviour

278 and of individual behaviour when in a group, thus addressing both features. In ants, the
279 average behavioural type of group members may be a key determinant of group
280 behaviour, as suggested by experimental work on social spiders showing that the group
281 'boldness' in prey capture behaviour reflects the average boldness of individuals across
282 the group (Pruitt et al., 2014).

283 There has been empirical evidence of a direct link between individual and
284 collective personality, especially in social insects, which constitute the most striking
285 example of organized collective behaviour (e.g., Modlmeier and Foitzik, 2011; Hui and
286 Pinter-Wollman, 2014; Cronin, 2015). However, this relationship has been also shown
287 in birds (Aplin et al., 2013; Aplin et al., 2014), fish and social spiders. In the guppy
288 (*Poecilia reticulata*), groups with shy and bold fish were faster in exploration of a novel
289 environment, and faster in sampling a foraging patch, than groups with only shy or bold
290 individuals (Dyer et al., 2009); in Atlantic salmon (*Salmo salar*), inactive individuals
291 kept the group inactive (Brown and Laland, 2002). An experiment using a similar
292 design as our ant study, created experimental groups of guppies following a gradient
293 based on a personality trait and found no significant correlations between group
294 exploratory behaviour and average group personality score (Brown and Irving, 2014). A
295 recent study on stickleback (*Gasterosteus aculeatus*) showed that individual personality
296 traits shape group functioning and performance, thus explaining the emergence of
297 collective behaviour from consistent individual differences (Jolles et al., 2017). Finally,
298 a study manipulating group composition in mosquitofish (*Gambusia holbroki*) found
299 that different degrees of repeatable locomotion behaviour in asocial condition were
300 partly maintained within groups. Moreover, the strength of individuality decreased with
301 increasing group size, indicating increased conformity (Cote et al., 2011). In our study,

group size was kept constant, but it would be interesting to test the possible influence of group-size on the relationship between individual and group personality in ants.

It is not clear whether natural colonies of social insects are composed by groups that are homogeneous for personality, by a mix of behavioural types, or whether they include individuals that exert a disproportionate effect. One possible limitation of our laboratory experiments is that such artificial small groups might not reflect the actual behaviour and group composition in a natural setting. However, most ant colonies start out small and some mature colonies experience fluctuations of group size, for instance after raids by social parasites or wars with neighbouring competitors. *Formica fusca* is a common host species of social parasites, both obligate (*Polyergus rugescens*) and facultative (*F. sanguinea*), the latter being particularly aggressive during raids and killing many host workers (d'Ettorre and Heinze, 2001). During these raids, it is very frequent that small group of workers escape and find themselves outside the nest, trying to save some cocoons from the pillage by the parasite. These workers have to regain the nest afterwards. There is also the case of polydomous colonies, where a small subset of workers may occur together in relatively isolated nest chambers. In addition, most ant species form subgroups of individuals during their normal activities (e.g., foraging and prey retrieval). An interesting example comes from the natural behaviour of the ant *F. schaufussi* in which "episodic" roles persist only for the duration of a single group performance (cooperative prey retrieval) and cannot be explained by genetic predispositions or age-polyethism (Robson and Traniello, 2002). However, ants do form subgroups of individuals during their normal activities (e.g., foraging) and we show here that, if homogeneous, their performance will directly reflect the average individual

contribution. Therefore, we predict that the recruitment of individuals of a subgroup that must perform a task could be non-random and based on personality traits.

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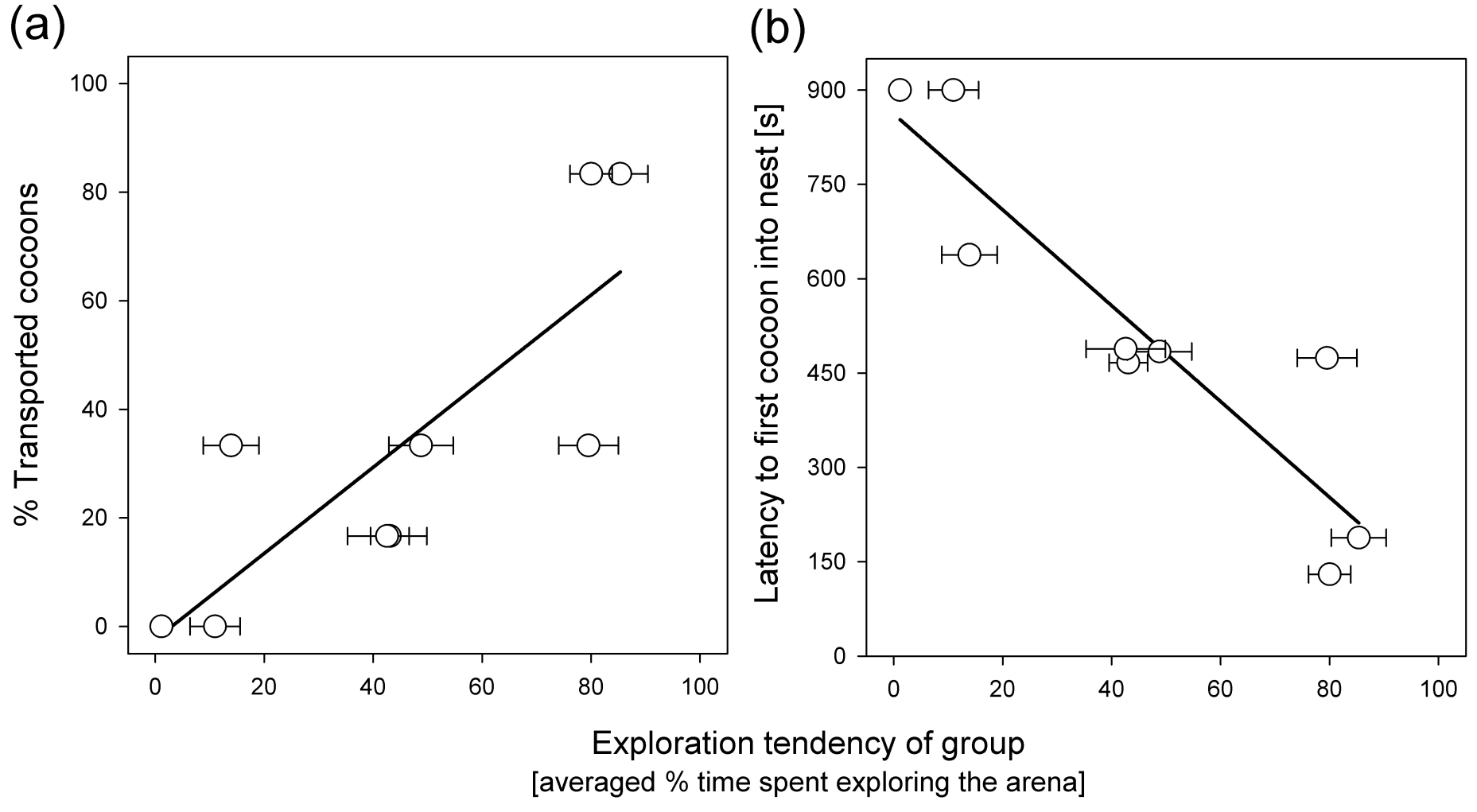
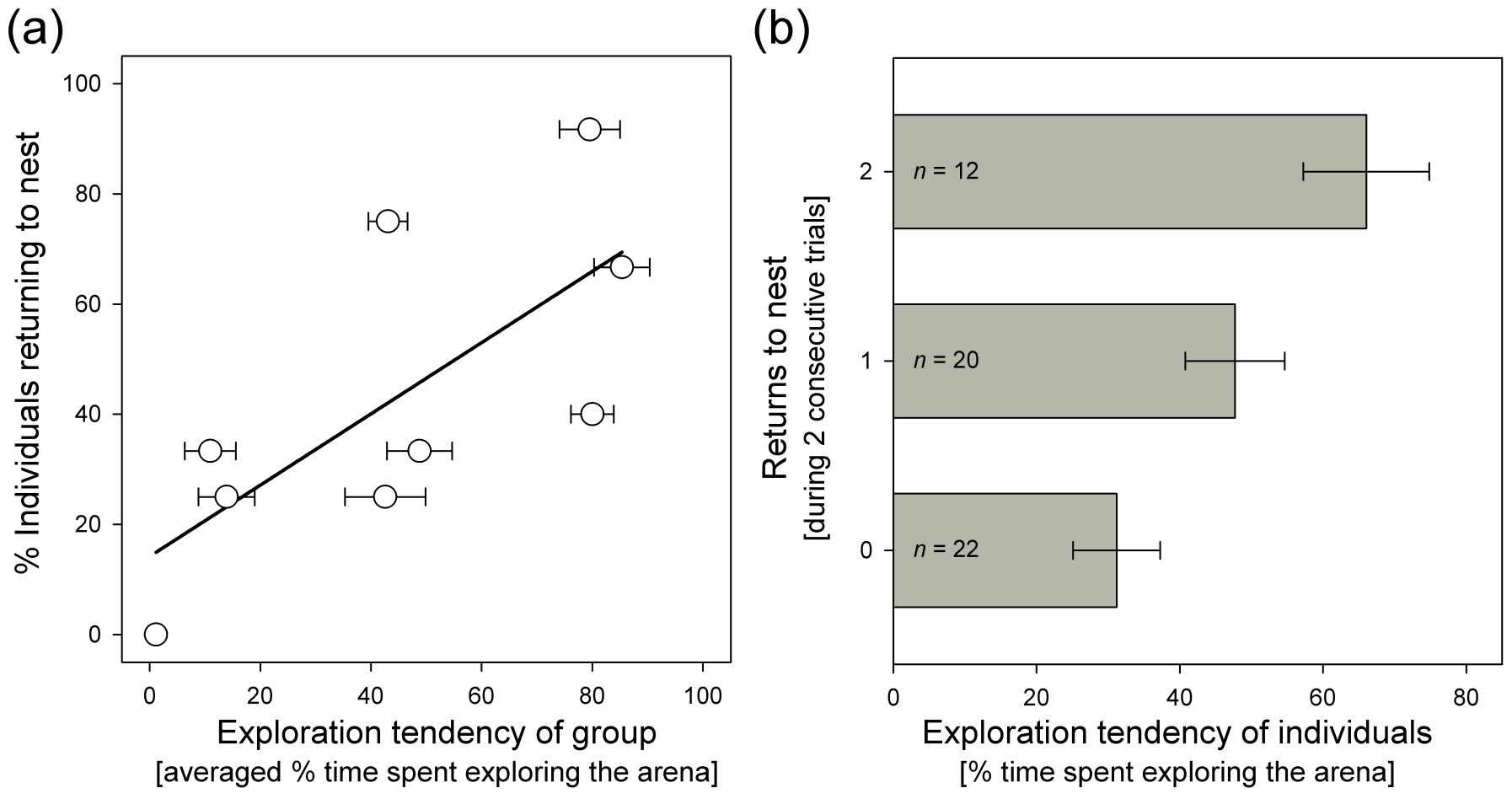
Figure legends

Figure 1. Group-level associations between the averaged (means ± SE) exploratory activity in groups of *F. fusca* composed of individuals with similar exploration tendencies and the latency (*a*) until the first cocoon was transported into an adjacent nest box and (*b*) the percentage of cocoons each group transported into the nest box. Variables obtained during group observations were quantified over two trials of 15 minutes each and were averaged for analysis. Three cocoons were offered per trial. Latency times of 900 s indicate that no cocoon was transported into the nest. Regression lines are based on parameter estimated of LMM including colony identity and group identity as random factors, see text for details.

Figure 2. (*a*) Group-level associations between the averaged (means ± SE) exploratory activity in groups of *F. fusca*, composed of individuals with similar exploration tendencies and the percentage of individuals per group entered the nest box. (*b*) Individual-level associations between exploratory activity (means ± SE) as determined by the percentage time the animals showed locomotor activity during prior open field tests and the number of returns to the nest (count variable with 3 levels: no returns to nest; returning to nest during one trial; returning to nest during both trials of the experiment). Analyses by LMM; see text for details.


(a)
% Transported cocoons
0
20
40
60
80
100
(b)
Latency to first cocoon into nest [s]
0
150
300
450
600
750
900
0
20
40
60
80
100
Exploration tendency of group
[averaged % time spent exploring the arena]


(a)
% Individuals returning to nest
0
20
40
60
80
100
Exploration tendency of group
[averaged % time spent exploring the arena]
(b)
Returns to nest
[during 2 consecutive trials]
2
1
0
n = 12
n = 20
n = 22
0
20
40
60
80
Exploration tendency of individuals
[% time spent exploring the arena]