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## Original Article

# Individual learning performance and exploratory activity are linked to colony foraging success in a mass-recruiting ant

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Learning plays an important role in the life of many animals. In social insects, colony foraging success depends on the combined actions of many individuals and learning contributes to individual foraging success. In many ants, for example, route learning helps foragers to navigate between the nest and a food source. Here, we studied if the foraging success of a colony depends on the route-learning performance of its individuals. We used a doubly bifurcating T-maze to assess the route-learning performance of ants from 12 *Lasius niger* colonies. We also measured the propensity of workers to deposit trail pheromone and to explore the surrounding of their nest. We then tested colony foraging performance in a complex maze, set up either as a poor environment (one food source at the end of one tip), or a rich environment (a food source at the end of each tip). We found that individual learning performance was linked to colony foraging success in the rich, but not the poor environment. The propensity of individual ants to lay pheromone correlated negatively with their learning performance and only predicted colony foraging success in colonies with poor learning abilities in a rich environment. The strongest predictor of colony foraging success was exploratory activity, which differed consistently between colonies. Our results suggest that the importance of individual learning for colony foraging success depends on the environment and that explorative activity is an important factor for colony foraging success.

**Key words:** collective foraging, *Lasius niger*, learning, pheromones.

## INTRODUCTION

Learning allows animals to acquire, remember, and use crucial information about their environment (Shettleworth 2010). Individuals that learn with a higher efficiency or accuracy are expected to make a better use of their environment, which is likely to increase their survival and, ultimately, fitness (Dukas and Bernays 2000; Cole et al. 2012). However, how exactly learning performance and cognitive abilities increase fitness has only recently become a focus of research (Dukas and Bernays 2000; Dukas 2008; Burns et al. 2011; Thornton et al. 2014). The few studies that have explored this link suggest that efficient learning positively affects fitness-related measurements: Keagy et al. (2009), for example, provide evidence for a positive relationship between male problem-solving ability and mating success in bowerbirds (*Ptilonorhynchus violaceus*) and Cole et al. (2012) showed that female

great tits (*Parus major*) that are better problem-solvers produced larger clutches.

In social insects, behaviors that are crucial for survival are often performed by different groups of workers. These behaviors include the building of the nest, defense against predators, taking care of the brood, and the collection of food to maintain the colony (Wilson 1971; Hölldobler and Wilson 1990, 2009). Foraging in particular requires constant learning as workers constantly need to acquire and process information about the characteristics of resources and the external environment (von Frisch 1967; Dukas and Visscher 1994; Wehner 2003; Giurfa 2007; Collett et al. 2013; Grüter and Leadbeater 2014; see Langridge et al. 2004 for an example in the context of nest migration). For example, foragers need to learn food odors, shapes, or how to handle flowers (Menzel 1985; Chittka and Thomson 1997; Chittka et al. 1999; Farina et al. 2005; Giurfa 2007; Grüter, Moore, et al. 2011). They also need to learn to navigate their environment to find food sources quickly and without getting lost (Collett et al. 2003; Beverly et al. 2009; Collett 2009; Lent et al. 2010; Collett et al. 2013). Thus, individual learning abilities should affect the colony's ability to take advantage of resources, which is likely to impact on the colony's reproductive

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output and survival. However, the link between individual learning and colony foraging success has rarely been investigated. A rare exception is a study showing that bumble bee (*Bombus terrestris*) colonies whose foragers were better at forming associations between artificial flower colors and food presence were also better at food collection in the wild (Raine and Chittka 2008). This study highlights that colonies often differ considerably in the learning abilities of their workers (see also Raine et al. 2006; Hoedjes et al. 2011) and raises the question how this effect depends on the environment, for example, the spatiotemporal distribution of food sources.

One major challenge that involves learning is the ability to return to a previously exploited food source. Insects rely mainly on 2 mechanisms to memorize routes (reviewed in Collett et al. 2003; Wehner 2003; Wystrach and Graham 2012; Collett et al. 2013). During the first visits to a food source, they use path integration to keep track of the distance and directions of their outwards journey. Simultaneously, they begin to store images of their path in their memory, which the animal uses to align itself on the way back to the food source by a process called image matching (Collett et al. 2013). Many social insects additionally use social information to locate food sources, either provided as cues (e.g., the presence of other individuals at food sources, Slaa et al. 2003; Leadbeater and Chittka 2005; Avargues-Weber and Chittka 2014) or signals (e.g., the waggle dance, von Frisch 1967; pheromone trails, Hölldobler and Wilson 1990). Foragers of the mass-recruiting ant *Lasius niger* use both route memory and social information in the form of pheromone trails to navigate during foraging (Aron et al. 1993; Evison et al. 2008; Grüter, Czaczkes, et al. 2011; Czaczkes et al. 2011; Czaczkes, Grüter, Ellis, et al. 2013; Czaczkes and Heinze 2015; Grüter et al. 2015). Pheromone trail information can also interact with memory to improve learning and increase walking speed, making this a powerful combination of information sources for foragers (Czaczkes et al. 2011; Czaczkes TJ, Czaczkes B, et al. 2015; Czaczkes, Grüter, et al. 2015). *Lasius niger* foragers with a reliable route memory will often prefer memory over pheromone information (Aron et al. 1993; Grüter, Czaczkes, et al. 2011), which further highlights the importance of route learning for foraging *L. niger*.

The interactions between 1) the dynamics of various forms of learning, 2) the ecological niche of a colony, and 3) colony fitness are likely to be very complex (e.g., Hoedjes et al. 2011; Mery 2013). Information about the relationship between particular learning tasks and colony behaviors that depend on these learning tasks represent an important basis to better understand how learning and ecology might affect colony success. The goal of the present study was to test if the individual route-learning performance of a colony's foragers is linked to colony foraging success in *L. niger*. We used a doubly bifurcating T-maze with 4 end points to test the ability of individual ants to learn the route to food sources. During the same tests, we also measured the tendency of workers of different colonies to explore their environment and to deposit trail pheromone while foraging. Additionally, the consistency across time of these colony-level traits was quantified to explore whether they form part of a collective "personality", that is, consistent between-colony differences in behavior (Wray et al. 2011; Jandt et al. 2014). We took these measurements while foragers were foraging alone because we wanted to quantify learning and pheromone deposition propensity in the absence of confounding interactions with nest mates. The behavior of foraging ants can be affected by different social cues and signals (e.g., trail pheromone, Hölldobler and Wilson 1990; Czaczkes, Grüter, et al. 2015; foot prints, Devigne and Detrain 2006; Czaczkes et al. 2011; or collisions: Dussutour

et al. 2004; Gordon 2010; Czaczkes, Grüter, et al. 2013; Pinter-Wollman et al. 2013) and disentangling the effects of different social factors on individual behavior would be difficult. Then, we tested if the average individual learning performance explained the foraging success of freely foraging colonies in a poor and a rich foraging environment. In the poor environment, colonies had access to one food source, placed at one end point of a triple T-maze. In the rich environment, colonies were given 8 food sources, one at each end point of the triple T-maze. We hypothesized that colonies with faster-learning ants perform better in the collective foraging experiment. Furthermore, we also expected that the tendency to lay trail pheromone and the exploratory activity of a colony positively affects colony foraging success.

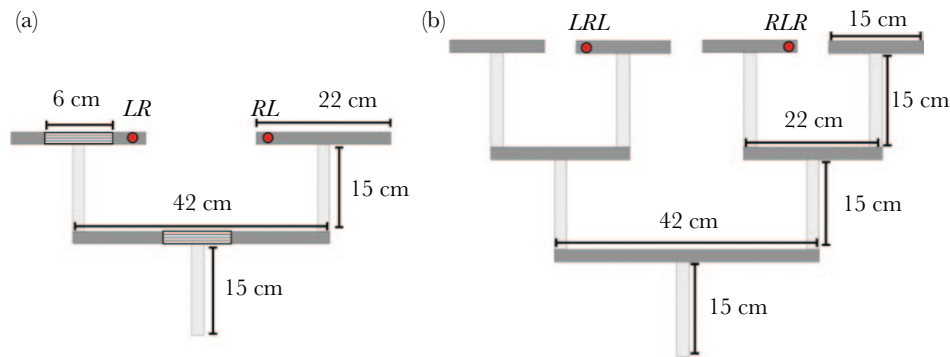
## METHODS

### Study species and maintenance of colonies

We collected 12 colonies of *L. niger* between April and May 2014 and performed the experiments between June and September 2014. All colonies were standardized (by counting of individual ants) to have 1200 workers per colony fragment, but no queen or brood. Queenless colony fragments (henceforth called "colonies" for simplicity) are routinely used in foraging experiments (Dussutour et al. 2005; Evison et al. 2008; Maillieux et al. 2010; Czaczkes, Grüter, Ellis, et al. 2013). Mortality of ants was not quantified but *L. niger* ants usually live ~1–3 years in the laboratory (Grüter C, personal observation) and the number of dead ants remained low during the course of our experiment. During the time of the experiment, colonies were housed in plastic boxes (25 × 11 × 38 cm) and maintained in constant conditions (14 h light; 10 h dark; 25 °C; 55% humidity). The bottom of each box was covered with a layer of plaster of Paris, and the walls were coated with Fluon to prevent ants from escaping. Nest boxes were provided in the form of medium sized petri dishes (9-cm diameter), partly filled with plaster of Paris and covered by a piece of paper. Colonies were fed 3 times a week with an artificial ant diet (Bhatkar and Whitcomb 1970) and *Drosophila melanogaster* once a week. Water was supplied ad libitum. In order to promote equally high levels of motivation to forage, food sources (except water) were removed from each colony 3 days prior to a trial.

### Experimental procedure: individual learning ability

Learning abilities in single ants were assessed using a double T-maze with 4 end points (similar to Czaczkes, Grüter, Ellis, et al. 2013; Grüter et al. 2015) (Figure 1a). In order to perform a learning trial, we connected the maze to the storage box with a paper bridge enabling the ants to enter the maze. To evaluate the *latency to discover the maze* of a colony, we recorded the time it took the first 5 ants to enter the maze at the beginning of each experiment trial using an HD camera (Panasonic HC-V130): We measured the time between the moment when the paper bridge touched the floor of the foraging box and the moment when the fifth ant crossed the paper bridge to enter the maze. A feeder containing 1 M sucrose solution, supplied ad libitum, was placed at one end point in the maze. For each ant, we chose one of 2 feeder locations which corresponded to difficult to learn paths, that is, left–right (LR) or right–left (RL) (Czaczkes, Grüter, Ellis, et al. 2013; Grüter et al. 2015) (Figure 1a). The first 2 ants that found the feeder were marked with an acrylic paint dot on their abdomen and were allowed to make



**Figure 1**

(a) Schematic representation of the double T-maze with 4 end points used during the individual learning tests. The feeders were placed at one of the 2 locations corresponding to difficult to learn paths, that is, left–right (LR) or right–left (RL); dashed areas show where pheromone depositions were counted. (b) Schematic representation of the triple T-maze with 8 end points used during the collective foraging experiments. In the rich environment, the feeders were placed at every end point, whereas in the poor environment, food was placed at one of the 2 locations corresponding to difficult to learn paths, that is, left–right–left (LRL) or right–left–right (RLR).

4 more visits to the feeder. Thus, the 2 marked ants were allowed to forage at the same time, whereas all other ants were removed from the maze and returned to the colony or prevented from entering the maze by lifting the bridge. We took note of the first end point (LL, LR, RL, or RR) that each marked ant reached on every trip from the nest to the food source. The maze was covered with pieces of paper ( $15 \times 2 \text{ cm}^2$ ). This allowed us to remove any pheromone deposition after each visit by replacing the pieces of paper with new ones. Thus, ants were forced to use their memory to find their way during their outwards trip (Czaczkes, Grüter, Ellis, et al. 2013; Grüter et al. 2015). The second ant was allowed in the maze only after the first ant had reached an end point to prevent any communication about the feeder location. During each visit in the maze, we counted the total number of pheromone depositions which occurred at both bifurcations within a 3-cm zone on both sides of the 2 stems (Figure 1a) when ants returned to the nest. *Lasius niger*'s pheromone laying behavior is easy to observe as the ant shortly stops to press the apex of its abdomen on the ground (Beckers et al. 1992). We focused on depositions of ants returning to the nest because ants deposit more pheromone on their homewards journeys (Czaczkes, Grüter, et al. 2013; Grüter et al. 2015).

The entrance and exit times from the maze were also recorded for each trip, which provided information about the amount of time each ant spent in the maze during a trip to the feeder. After a total of 5 visits (4 return trips), the ants were removed from the colony. We tested 16 ants in each colony, 8 of them were assigned to the RL situation and the 8 others to the LR situation. The same protocol was used 2 months later with different ants, after the collective foraging test (see below), to check for consistency of route learning, activity level (see below), and pheromone deposition at colony level. Thus, during those 2 separate *individual learning* periods (learning test periods 1 and 2), we tested a total of 32 ants for their learning performance and pheromone deposition rate in each colony.

### Experimental procedure: collective foraging

After the first test period of individual learning, we assessed the collective foraging performance with a triple T-maze (Figure 1b). We increased the complexity of the maze for the *collective foraging* part (3 bifurcations) in order to increase the learning difficulty and, thereby, make effects of learning differences between colonies easier to detect. A previous study found that learning performance and pheromone

deposition rate correlate across bifurcations: The proportion of correct decisions made by the foragers of a colony at the first bifurcation shows a strong positive correlation with the proportion of correct decisions at the second bifurcation (Spearman rank correlation: first vs. second bifurcation:  $r_s = 0.83$ ,  $P = 0.015$ ,  $N = 8$  colonies; Grüter C, unpublished data). Likewise, the number of pheromone depositions made by the foragers of a colony at the first bifurcation shows a strong positive correlation with the number of pheromone depositions at the second bifurcation ( $r_s = 0.95$ ,  $P = 0.001$ ,  $N = 8$  colonies; Grüter C, unpublished data). Thus, we are confident that the learning performance and pheromone deposition rates measured in a double T-maze would be a good predictor of the learning performance and pheromone deposition rate in a triple T-maze.

In order to perform an experimental trial, we connected the maze to the storage box using a paper bridge. Feeders containing 1 M sucrose solution, supplied ad libitum, were placed either at one end point in the maze (poor environment), or at every end point (rich environment). Feeders were large enough to avoid crowding effects (Grüter et al. 2012). We chose 2 different feeder placements for the poor environment, left–right–left (LRL) and right–left–right (RLR). This alternating route is likely to represent a difficult to learn route (Czaczkes, Grüter, Ellis, et al. 2013; Grüter et al. 2015). Each colony was tested twice in both the rich and the poor environment (once with the feeder at LRL and once at RLR). During a test, colonies were allowed to forage freely in the maze during 40 min. Colonies of this size often become satiated after this period (see, e.g., Grüter et al. 2015, their Figure A1). Every 10 min, we recorded 2 types of data. First, we measured foraging success by counting the number of workers simultaneously drinking at the feeders, using still images taken by a high definition camera (Panasonic HC-V130 camera). Furthermore, we evaluated a colony's *latency to food discovery* by recording the time it took until the first 3 ants discovered a feeder.

### Activity level

In addition to the 2 previously mentioned measures of exploratory activity (*latency to discover the maze* and *latency to food discovery*), we quantified the number of ants walking over a piece of cardboard inside the storage box, called *activity level*: 2 weeks prior to the start of the first experiment, we placed in each storage box a  $5 \times 5 \text{ cm}^2$  piece of cardboard in the corner diagonally opposed to the nest

box (approximately 40 cm distance). Before each experimental trial, and during both individual and collective experimental phases, we filmed (Panasonic HC-V130 camera) the piece of cardboard and counted the number of ants walking over it during 1 min. This number of ants walking over the cardboard piece was used to evaluate the explorative activity of a colony in the immediate surrounding of the nest.

## Statistical analysis

Data analysis was performed using generalized linear mixed-effect models (GLMMs) and linear mixed models (LMEs) (Zuur et al. 2009) in R 2.14.2 (R Core Team 2013). We used the lme4 package (Bates et al. 2015) and its glmer and lmer functions. We used LME for normally distributed response variables (colony learning score) and GLMMs for variables following a Poisson distribution (number of ants at a feeder, time spent in maze, *latency to food discovery*) (Zuur et al. 2009). “Colony” and “trial” were included as random effects to control for nonindependence of values from the same colony and the same trial (Zuur et al. 2009).

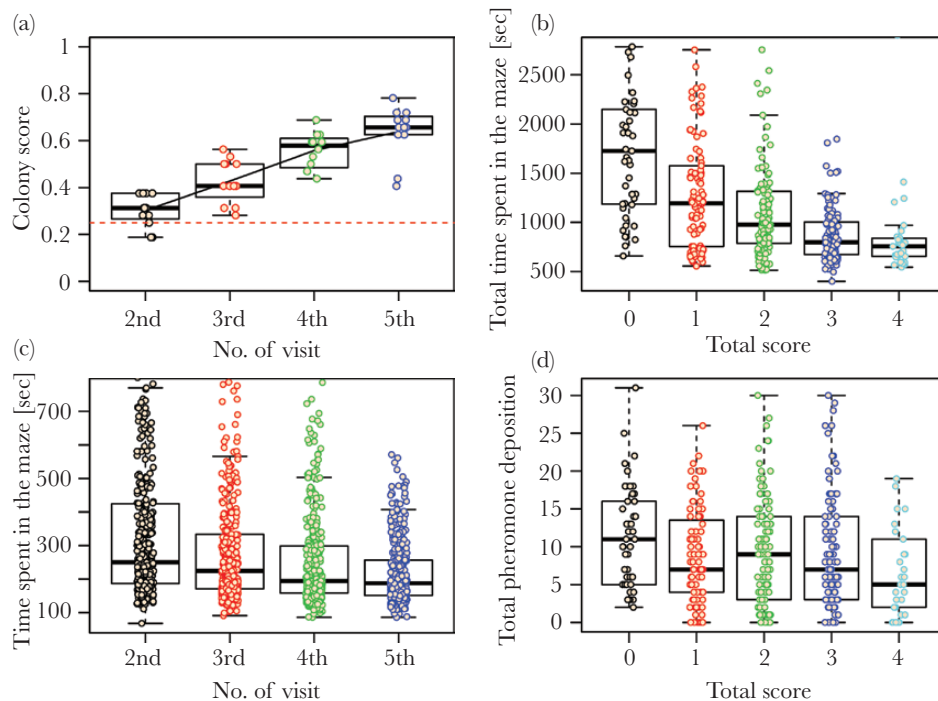
We performed the analysis of foraging success separately for the poor and the rich environment. To quantify the learning performance of a colony, we calculated the proportion of all ants tested in the colony navigating to the correct end point during the final training trip (resulting in a value between 0 and 1 = “learning score” for each colony). The learning score and pheromone deposition rate were averaged over the 2 individual learning experiments and used as explanatory variables in the models analyzing colony foraging success. The *activity level* of the colony during the collective foraging experiments was also included as an explanatory

variable. Only *activity level* was included as a measure of explorative activity because it correlated highly with the other 2 measurements of exploration (*latency to discover the maze* and *latency to food discovery*). All continuous predictors were centered by subtracting the mean to facilitate the interpretation of significant terms in the presence of significant interactions (Quinn and Keough 2002). The variable *activity level* had a substantially larger mean and variation than the other predictors, which caused problems when running the models. To avoid this, we log-transformed this variable before centering. Two-way interactions were tested, and nonsignificant interactions were removed for the final model (Zuur et al. 2009). The colony-level consistency of learning performance, pheromone deposition, and exploratory activity in the 2 individual learning phases was quantified by calculating the Pearson product-moment correlation coefficient  $r$ . A high correlation coefficient, for example, for learning performance would indicate that the average learning performance of the foragers of a colony during learning test period 1 would be similar to the average learning performance of foragers of the same colony during learning test period 2.

## RESULTS

### Individual learning

Overall, we found that ants learned the route: There was a positive relationship between the number of visits to the feeder and the proportion of ants that made correct decisions at the bifurcations (LME,  $t = 11.46$ ,  $P < 0.0001$ ,  $N = 12$  colonies; Figure 2a). We then tested if learning helped ants to increase their foraging speed and found a negative relationship between the time ants spent in



**Figure 2**

(a) The average learning score of 12 *Lasius niger* colonies, separately for all 4 visits. The black line shows the mean score at each visit. The red dashed line represents the random expectation, that is, if ants had chosen each end point randomly, they would have obtained a score of 0.25 on average. Colored dots show individual data points. (b) The time ants spent in the maze depending on the total score of an ant (0–4). Four means that an ant never made a mistake during the 4 trips; 0 means that an ant never made a correct decision during the 4 trips. Sample sizes were as follows: score = 0,  $N = 46$ ; score = 1,  $N = 95$  ants; score = 2,  $N = 115$  ants; score = 3,  $N = 98$  ants; score = 4,  $N = 30$  ants. (c) The time ants spent in the maze during each of the 4 visits. (d) The relationship between the learning score of an ant and its pheromone deposition rate. Boxplots show the median, quartiles, the 5th and 95th percentiles.



the maze and the total score (number of correct decisions per ant, 0–4) obtained during the 4 trips (GLMM,  $z = -120.9$ ,  $P < 0.0001$ ). Thus, the best learners were also the fastest in the maze (Figure 2b). A link between learning and foraging speed is further suggested by a negative relationship between the number of visits to the feeder and the time spent in the maze during a visit (GLMM,  $z = -154.5$ ,  $P < 0.0001$ ). Thus, the time ants spent in the maze decreased with the experience acquired during previous trip to the food source (Figure 2c). We then tested if individual learning performance affects the propensity to lay pheromone and found that better learners lay less pheromone (GLMM,  $z = -3.1$ ,  $P = 0.0016$ ) (Figure 2d).

Estimates of colony-level consistency of learning ability, pheromone deposition, and *activity level* across the 2 individual learning test periods revealed differences in the consistency of these measurements. We obtained a correlation coefficient of 0.3 for average colony learning ability, 0.68 for the pheromone deposition rates, and 0.62 for *activity level*.

### Collective foraging: latency to food discovery

We first tested if *activity level* and the type of environment (poor vs. rich) affected the *latency to food discovery*. We found a negative relationship between *activity level* and the *latency to food discovery* (GLMM,  $z = -8.26$ ,  $P < 0.0001$ ). Colonies that were more active inside their boxes discovered food sources faster. The type of environment (poor vs. rich) also affected the time it took ants to discover food ( $z = -40.58$ ,  $P < 0.0001$ ): If food was abundant, ants found food more quickly without prior knowledge of the maze. Furthermore, we found a highly significant interaction between the environment type and *activity level* ( $z = 11.11$ ,  $P < 0.0001$ ) in predicting the *latency to food discovery*. The *latency to food discovery* decreases as the *activity level* goes up, but this effect is stronger when food is more difficult to find (estimated  $R^2 = 0.18$  in poor environment vs. 0.03 in rich environment) (Figure 3b).

### Collective foraging: colony foraging success

*Activity level* and the *latency to discover the maze* showed a strong negative relationship ( $z = -19.98$ ,  $P < 0.0001$ ; Figure 3a): Colonies with higher *activity level* found the maze in less time. Thus, *activity level*, *latency to food discovery*, and the *latency to discover the maze* are highly correlated measurements of the explorative activity of a colony, and we only included *activity level* as a predictor of colony foraging

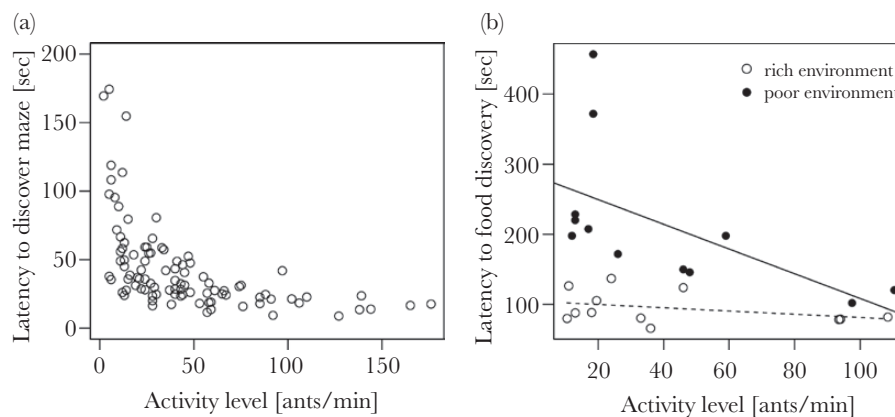
success. Additionally, we used average colony learning ability (colony score) and average colony pheromone deposition rate as predictors and the number of ants at the feeders as the response variable.

In the rich environment, learning performance and *activity level* (Figure 4) positively affected the number of ants at the feeders, whereas pheromone deposition per se had no significant effect (Table 1). However, the model revealed a significant interaction between learning performance and pheromone deposition (Table 1). The slope of this interaction was negative, suggesting that the effect of pheromones is stronger as learning gets poorer. We also found a significant interaction between pheromone deposition and *activity level*. The slope was again negative indicating that pheromone deposition rate is of increasing importance in colonies with a lower *activity level*. These interactions mean that the main effects are less straightforward to interpret (Quinn and Keough 2002; p. 130–132). Given that all predictors were centered we can conclude that the learning score has a positive effect on foraging success in colonies with average *activity level*. *Activity level*, in turn, has a positive effect on foraging success in colonies with average pheromone deposition rates.

In the poor environment, neither average learning performance nor the average pheromone deposition rate of colonies predicted the number of ants at the feeders (Table 1). However, *activity level* again had a positive effect (all interactions were not significant) (Figure 4).

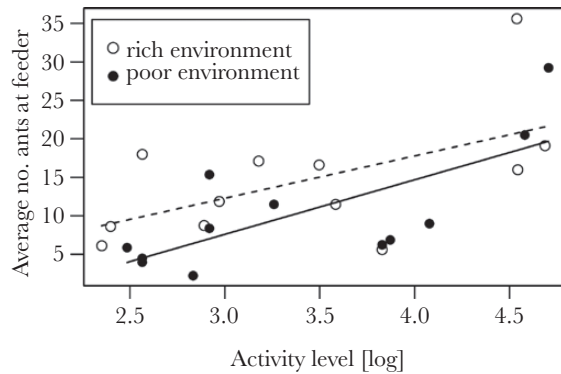
## DISCUSSION

We found that individual learning performance showed a positive association with colony foraging success in a rich, but not in a poor environment. This seems counterintuitive because navigational mistakes would often still lead to a food source in the rich environment. However, previous studies have found that one effect of route learning is an increase in foraging speed (Czaczkes et al. 2011; Grüter et al. 2015; our Figure 2b,c). As a consequence, faster learners require less time to navigate in the maze (Figure 2b). This means that they return to the feeder in less time and collect more food per time unit. This learning effect should also improve colony foraging performance in a poor environment, but the overall smaller number of foraging ants in the poor environment (see Figure 4) means that this effect is likely to be weaker at the colony level and, therefore, harder to detect in an environment with only 1 food source.



**Figure 3**

(a) The latency to discover the maze (in seconds) as a function of the activity level measured during the learning performance tests (8 measurements per colony). (b) Latency to food discovery as a function of mean activity level (average for each colony) in the poor and the rich environment. The lines represent the best-fit lines of the relationship between the latency to food discovery and activity level in the rich (dashed line) and the poor (black line) environment.



**Figure 4**

The relationship between activity level (log-transformed as in model) and the number of ants drinking at the feeder(s) during the collective foraging experiment. Values were averaged for each colony. The lines represent the best-fit lines estimated with a linear model using colony averages (dashed line = rich environment; continuous line = poor environment).

**Table 1**

**Summary of the collective foraging experiment**

Predictor	<i>z</i> value	<i>P</i> value
Rich environment		
Learning score	3.14	0.002
Activity level	6.78	<0.0001
Pheromone deposition rate	0.02	0.98
Learning score × pheromone deposition	-2.88	0.004
Activity level × pheromone deposition	-5.12	<0.0001
Poor environment		
Learning score	1.41	0.16
Activity level	9.8	<0.0001
Pheromone deposition rate	-0.09	0.93

Two separate models were run for the rich and the poor environment. Results are shown for all terms included in the final models. Nonsignificant interaction terms were removed for the final models (Zuur et al. 2009).

The relationship between learning performance and foraging success in nature is probably not straightforward, and it has been suggested that navigational errors could even be beneficial in certain environments (Deneubourg et al. 1983; Evans and Raine 2014). In rapidly changing environments, for example, taking an incorrect route could lead to the discovery of a new profitable patch to exploit.

Colony foraging performance strongly depended on activity levels inside the nest box, measured as the number of ants walking over a piece of cardboard. This activity level, in turn, was highly correlated with the latency to enter the maze and discover the food (Figure 3). These results suggest that the tendency of ants to run around in the vicinity of their nest box is related to their tendency to both enter and explore a novel environment. The importance of individual explorative activity for colony foraging success has rarely been investigated, but a recent study on collective nest choice in *Linepithema humile* found that the presence of more explorative individuals had a positive effect on both the speed and accuracy of nest choice (Hui and Pinter-Wollman 2014). Furthermore, simulations suggest that increased exploration might improve information about foraging opportunities by increasing social interactions among nest mates (Pinter-Wollman et al. 2011). It is tempting to conclude that exploratory activity of colonies is more important for colony fitness than learning performance. However, increased exploratory activity

might come at a considerable energetic cost in environments with few food sources because a large number of foragers might be running around without discovering food sources. Furthermore, even modest learning effects might be important if they accumulate in the naturally much larger colonies and over long time periods. On the other hand, forming and maintaining an accurate memory can also impose costs and might have to be traded-off with other physiological processes (Mery and Kawecki 2005; Burns et al. 2011). Trade-offs with other fitness-related traits could help to explain the maintenance of natural variation in learning performance (Burns et al. 2011).

The propensity of individuals to deposit trail pheromone had a surprisingly small effect on the number of foraging ants during the collective foraging period. Average deposition rate was not significant as the main effect in either environment. Interestingly, pheromone deposition rate interacted with both learning performance and activity levels in the rich environment. When food sources were abundant, pheromone depositions were increasingly important in colonies with lower learning scores. Thus, colonies might be able to compensate for a poor learning ability of its foragers by laying more pheromone. This interpretation is consistent with our finding that individual workers with poorer learning deposit more pheromone (Figure 2d). *Lasius niger* ants are able to evaluate the quality of their private information (route memory) about food source locations and increase pheromone deposition rate after making navigational mistakes (Czaczkes, Grüter, Ellis, et al. 2013; Czaczkes and Heinze 2015). Pheromone deposition rate of ants returning to the nest also seemed to be more important for colonies with a lower activity levels. As the activity level was linked with the latency to enter the maze, it is possible that colonies compensated for their low explorative activity by laying more pheromone once a food source had been discovered.

In *L. niger*, both route memory and pheromones play an important role in foraging (Aron et al. 1993; Evison et al. 2008; Grüter, Czaczkes, et al. 2011; Czaczkes, Grüter, Ellis, et al. 2013; Grüter et al. 2015). Further insight into the adaptive significance of individual learning and communication could be gained by studying species that rely more heavily on route learning, as appears to be the case in *Pogonomyrmex maricopa* (Hölldobler 1976) or *Formica rufa* (Rosengren and Fortelius 1986) versus species that rely more on pheromone trails, for example, the mass-recruiters *Monomorium pharaonis* (Robinson et al. 2008) or *Linepithema humile* (Aron et al. 1993). We would predict that the strength of the link between individual learning/pheromone deposition and colony foraging success depends on the importance that these 2 information source play in a species.

We found that learning performance had a colony-level consistency of 0.3 across the 2 learning periods (Pearson product-moment correlation coefficient). This relatively low correlation coefficient could be explained by an ongoing adaptation of ants to laboratory conditions, for example, caused by the experimental reduction in colony size. In the wild, *L. niger* workers live in much larger colonies (estimated mean colony size of 24000 workers) (Fjerdingsstad et al. 2003). It is possible that the abrupt change in colony size had an ongoing effect on worker motivation, which in turn can affect learning performance (e.g., Scheiner et al. 2005). In *Myrmica punctiventris*, for example, colony size influences the speed of ants on their homewards journey after visiting a food source (Herbers and Choiniere 1996). Learning performance could also be influenced by seasonal effects (in honey bees: Ray and Ferneyhough 1997). Finally, it is possible that a larger sample size during the individual learning periods would have provided higher

estimates of consistency. The relatively low consistency could also explain why we did not find stronger overall effects of learning performance on colony foraging success during the collective foraging period. The consistency of activity (number of ants walking over a cardboard piece,  $r = 0.62$ ) and pheromone deposition ( $r = 0.68$ ) was considerably higher, which indicates that they are not influenced by the same variables as learning performance or that they have a higher intrinsic consistency. In their meta-analysis, Bell et al. (2009) found that different types of behaviors differ considerably in their repeatability. It would be interesting to repeat these tests with other ant species to explore whether there are patterns in how consistent different behaviors are.

There has been much recent interest in the adaptive significance of colony personalities (e.g., Wray et al. 2011; Pinter-Wollman 2012; Jandt et al. 2014; Jongepier et al. 2014). Our data support the hypothesis that consistent behavioral differences between colonies affect fitness relevant traits, such as the ability to exploit food sources en masse, but our study also highlights the complexities in the relationship between individual learning, ecological circumstances, and colony success.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Pasquier and Grüter (2016).

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