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Colonies of ants allocate exploratory individuals to where they are ecologically needed

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Abstract

Individual differences in behavior have large consequences for the way in which ecology impacts fitness. Individuals differ in how they explore their environment and how exploratory behavior benefits them. In group-living animals, behavioral heterogeneity can be beneficial because different individuals perform different tasks. For example, exploratory individuals may discover new food sources and recruit group members to exploit the food, while less exploratory individuals forgo the risks of exploration. Here we ask how individual variation in exploratory behavior affects the ability of Argentine ant *Linepithema humile* colonies to (1) locate novel food sources, (2) exploit known food resources, and (3) respond to disruptions while foraging. To address these questions, we conducted field experiments on *L. humile* foraging trails in which we manipulated food availability near and at the foraging trails and disrupted the foraging trails. We sampled individuals based on their response to the perturbations in the field and tested their exploratory behavior in the lab. We found that exploratory individuals benefit the colony by locating novel foods and increasing resource exploitation, but they do not play an important role in the recovery of a foraging trail after disruption. Thus, the benefits of behavioral heterogeneity to the group, specifically in exploratory behavior, differ across ecological contexts.

Key words: exploration, foraging, individual variation, novel resources, recruitment, resilience.

Individual differences in behavior are prominent throughout the animal kingdom (Sih et al. 2004; Réale et al. 2007; Stuber et al. 2022). Individuals within a group may differ in their aggression toward conspecifics, latency to interact with predators, and foraging behavior (Sol et al. 2001; Wolf et al. 2007; Griffin and Guez 2014; Jolles et al. 2020). In groups of animals, such variation in behavior can influence the way in which groups operate (Sol et al. 2001; Griffin and Guez 2014; Jolles et al. 2020). Individual variation in foraging behavior impacts the way in which groups consume novel resources (Kurvers et al. 2009; Lemanski et al. 2021), make collective foraging decisions (Cook et al. 2020), and arrive at new food sources (Kurvers et al. 2009). Thus, the behavioral composition of a group, or a population, can impact the fitness outcomes of all individuals.

Variation among individuals in exploratory behavior is important in many ecological situations. Exploratory behavior is the movement of animals when traveling into a novel area, which allows them to gain personal knowledge about the new location (Verbeek et al. 1994; Dingemanse et al. 2007; Réale et al. 2007). Variation in exploratory behavior within a group of animals can impact the way in which groups find new resources and avoid predators. For example, highly exploratory three-spined stickleback individuals facilitate rapid collective group escape from predators (Ioannou and Dall 2016) and exploratory meerkats are more vigilant than less exploratory individuals (Gall and Manser 2018). Groups of *Linepithema humile* ants with a larger proportion of exploratory individuals are faster and more accurate when locating a new nest site relative to groups with few exploratory individuals (Hui and Pinter-Wollman 2014). Here we ask which other ecological situations are impacted by variation in exploratory behavior in *L. humile*. Specifically, we examined the importance of variation in exploratory behavior for the detection of novel food sites, response to a change in food availability at a known food site, and recovery of foraging in response to a disruption. We hypothesize that the importance of exploratory behavior will differ across these ecological situations.

Group-living animals may benefit from having exploratory individuals that discover and recruit to new food resources (Liker and Bokony 2009; Ashton et al. 2019). Highly exploratory individuals in a group are often referred to as innovators, scouts, and information producers, and less exploratory individuals are called followers, recruits, and scroungers (Barnard and Sibly 1981; Giraldeau et al. 1994; Aplin and Morand-Ferron 2017). The ratio of exploratory to non-exploratory individuals can have important consequences for the group, such as maximizing energetic efficiency in groups of house sparrows (Barnard and Sibly 1981), and impacting honey bee colonies' ability to locate new resources (von Frish 1967; Biesmeijer and de Vries 2001; Mosqueiro et al. 2017; Cook et al. 2020; Lemanski et al. 2021). In *L. humile*, some individuals leave the main foraging trail and recruit other ants from the foraging trail to new food sources (Flanagan et al. 2013). However, whether any ant from the foraging trail is likely

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to perform this behavior or whether only highly exploratory individuals deviate from the foraging trail is unknown. We predict that ants that tend to meander off the trail and find new food will show higher exploratory behavior in a controlled lab setting compared to ants that remain on the foraging trail that leads to familiar food.

Exploratory behavior may be beneficial when exploiting known food resources. Changes in food availability lead to changes in recruitment to food sources (Gordon 1991; Seeley et al. 2000). The ability to regulate how many individuals visit each food site is essential for maximizing resource acquisition in different environments (Sherman and Visscher 2002; Dornhaus et al. 2006; Lemanski et al. 2021). Social animals often regulate foraging activity based on food abundance. For example, harvester ants change their collective foraging behavior in response to the rate at which successful foragers return to the nest with food (Schafer et al. 2006; Gordon et al. 2008; Greene et al. 2013; Pinter-Wollman et al. 2013). Similarly, honey bees use the waggle dance to regulate collective foraging activity (von Frish 1967; Seeley et al. 2000). In *L. humile*, variation in exploratory behavior is linked with foraging trail usage, with highly exploratory individuals found at low-use trails and individuals with low exploratory behavior found at high-use foraging trails that lead to plentiful food sources (Page et al. 2018). However, it is unknown whether the allocation of exploratory individuals changes on these foraging trails in response to a rapid change in food abundance. We predict that when food availability increases rapidly, the proportion of exploratory individuals that are foraging will change—either increase to facilitate recruitment to the added food or decrease because exploitation of resources on an established trail does not require recruitment.

Finally, exploratory behavior may relate to the group's ability to respond to disruptions while foraging. Animals are susceptible to predation, competition, and other threats or disturbances that may hinder foraging. Individuals that differ in their exploratory behavior may respond differently to such disturbances (Stamps 2007; Wolf et al. 2007). For example, older and exploratory Asian elephants cross roads more readily than younger and less exploratory individuals (Mizuno et al. 2017), and bolder three-spined sticklebacks return to foraging faster than shy individuals after predator disruption (Ward et al. 2004). In *L. humile*, when a foraging trail is disturbed, foraging activity resumes after some time (Suckling et al. 2008). A link between exploratory behavior and response to disruptions may allow groups to balance a tradeoff between risk-taking during exploration, which may facilitate finding new resources but can expose individuals to predation, and metabolic costs and risk aversion, which may reduce the likelihood of finding new resources and reduce risks. Therefore, we predict that the first individuals to reestablish a foraging trail after disturbance will be more exploratory than individuals that avoid the disrupted area.

The Argentine ant, *L. humile*, is a successful invasive species (Suarez et al. 2001) partially due to its efficient foraging that can support large colonies (Human and Gordon 1999; Suarez et al. 1999). The foraging network of a colony consists of prominent foraging trails (Flanagan et al. 2013) that vary in usage intensity. Individuals from low-use trails demonstrate high exploratory behavior, while individuals from high-use foraging trails have low exploratory behavior, when tested for exploratory behavior in the lab using the same behavioral assay we employ in the current study (Page et al. 2018). Low-use trails can be established from existing high-use trails, allowing for fast recruitment to new food sources (Flanagan et al. 2013). Discovering which ants are responsible for establishing these new trails, responding to changes in food availability, and recovering from disruption to the foraging trail will help uncover what makes *L. humile* a successful invader.

Here, using experimental manipulations of *L. humile* foraging trails and assaying individuals for exploratory behavior, we ask if colonies allocate individuals with different behavioral types to where they are needed. First, we ask whether individuals that deviate from an established, high-use foraging trail are more exploratory than individuals who conform to the foraging trail. Second, we ask how the allocation of exploratory ants to a foraging trail changes in response to an increase in the amount of food the foraging trail leads to. Third, we asked whether exploratory individuals facilitate the reestablishment of a disturbed foraging trail.

Materials and Methods

Collection and handling of ants

We located foraging trails of *L. humile* in and around the UCLA Mildred E. Mathias Botanical Garden from April to August 2021. Foraging trails were initially chosen opportunistically and were used in our experiments if ant traffic was high, that is, "trail rate" was characteristic of a high-use trail: We determined "trail rate" by drawing an imaginary line through the foraging trail and counting the number of ants that crossed this line for 30 s; if 20 ants or more crossed this line in 30 s, we classified the trail as high use. We used a threshold of 20 ants based on Page et al. (2018), who categorized low-use trails as trails with fewer than 10 ants per 30 s and high use as trails with more than 20 ants per 30 s. Low-use trails were not sampled in this study. After the initial selection of foraging trails, we attempted to return to the same trails for subsequent experiments (for study questions 1 and 3), but only experimented on them if they exceeded the "high-use" trail rate threshold of 20 ants per 30 s. We selected which ants to collect based on the hypothesis being tested, as detailed below. All ants were collected with an aspirator. After collecting the ants, we brought them back to the lab, quantified their exploratory behavior, and released them back outside (rather than sacrifice them), within 50 m of where they were collected (which is within the range of an effective colony [Heller et al. 2008]), all on the same day.

Deviating from foraging trail

To test whether ants that deviate from a foraging trail are more exploratory than ants that conform to the foraging trail, we collected ants that arrived at a sugar bait placed near the trail. A sugar bait was a piece of cotton soaked in sugar water at a concentration of approximately 50%. We placed the bait at 1 of 3 distances from the trail—7, 14, and 21 cm—to determine whether individuals that are more exploratory deviate further from the trail (Figure 1). Only one bait distance was tested each day. The high-use trails that we sampled persisted for the duration of the experiment, thus each high-use trail was tested for all bait distances. All distances were tested in the same order for each trail (7 cm, 14 cm, and then 21 cm) not necessarily on consecutive days, see data in Supplementary Materials for details on exact sampling regime. We collected the first 10 ants that arrived at each bait and classified them as ants that deviate from the main trail. By collecting the ants

as soon as they reached the bait, we avoided testing individuals that were recruited to the bait from the foraging trail (Flanagan et al. 2013). To obtain ants that conform to the foraging trail, we haphazardly collected 10 more ants from the foraging trail. To minimize disruption to the foraging trail while collecting ants from the bait, we collected ants from the trail immediately after the 10 ants were collected from the bait at a location on the trail that was adjacent to the bait. In total, for each trail, we collected 10 ants from a sugar bait at each of the 3 distances, and 10 ants from the trail when each bait distance was tested, totaling 30 ants from the trail itself. We collected ants from 5 different foraging trails for this experiment for a total of 300 individuals: 30 ants from the baits and 30 ants from the foraging trail for each trail.

Response to food supplementation

To test whether supplementing food onto a foraging trail decreases the proportion of exploratory individuals on the trail, we placed a sugar bait at the foraging trail. A sugar bait was a piece of cotton soaked in sugar water at a concentration of approximately 50%. We placed the bait as close as possible to the trail (<1 cm) without disrupting the flow of foragers and close enough for the ants to detect and access it. Before placing the bait, we collected haphazardly 40 ants from the trail. After setting the bait, we collected 10 ants from the trail every 15 min for 60 min and measured the trail rate at each time point, before collecting the ants (Figure 1). Change in the proportion of exploratory individuals on the foraging trail can be achieved in three ways: (1) change in trail rate but no change in the number of exploratory individuals, (2) increase (or decrease) in trail rate and decrease (or increase) in the number of exploratory individuals on the trail, and (3) no change in trail rate but change in the number of exploratory individuals on the trail. We repeated this experiment on 7 trails and 400 individual ants.

Response to disturbance on trail

To test whether exploratory individuals reestablish a foraging trail after it is disrupted, we disrupted foraging trails by brushing ants off from the trail until there were no ants crossing the area of disturbance (approximately 10–15 cm of the trail) for at least 1min. The disrupted trails were all located on dirt, so while brushing the ants off the trail, we swiped the dirt as well, thus removing the pheromone trail. Before we disturbed the trail, we collected a random sample of 10 ants from the trail at the location where the disturbance occurred later. After the trail was disrupted, we collected the first 10 ants that crossed the midpoint of the disturbed area and 10 ants that reached the disturbed area and turned around (Figure 1). We repeated this sampling regime 1–2 times each day at 5 different trails. If we conducted 2 disturbances on the same day, they occurred at least 25–30 min apart and were at least 1 m from each other, and thus we considered them as independent samples because the foraging trail had been completely reestablished by then. The trail rate was measured before each disturbance. If the trail rate dropped below 20 ants per 30 s (see details on setting this threshold above), we did not conduct a trail disturbance, and therefore not all trails could be sampled more than once. The total sample size for this experiment was 210 individual ants from 5 trails.

Exploratory behavior

We quantified the exploratory behavior of individual ants using an 8-arm maze with unique spices at the end of each arm (Figure 1), following the methods in Modlmeier and Foitzik (2011), Hui and Pinter-Wollman (2014), and Page et al. (2018). Exploratory behavior measured in this assay is highly repeatable and is an efficient predictor of exploration in an open arena (Page et al. 2018). We placed an individual ant in the center of the maze and counted the number of times it visited any of the maze arms during a period of 5 min. We defined a visit to a maze arm as an ant moving 1 body length or more into the maze arm. The apparatus was cleaned with ethanol after each trial to ensure that any pheromones left by ants that were tested did not impact the behavior of subsequent individuals placed in the apparatus.

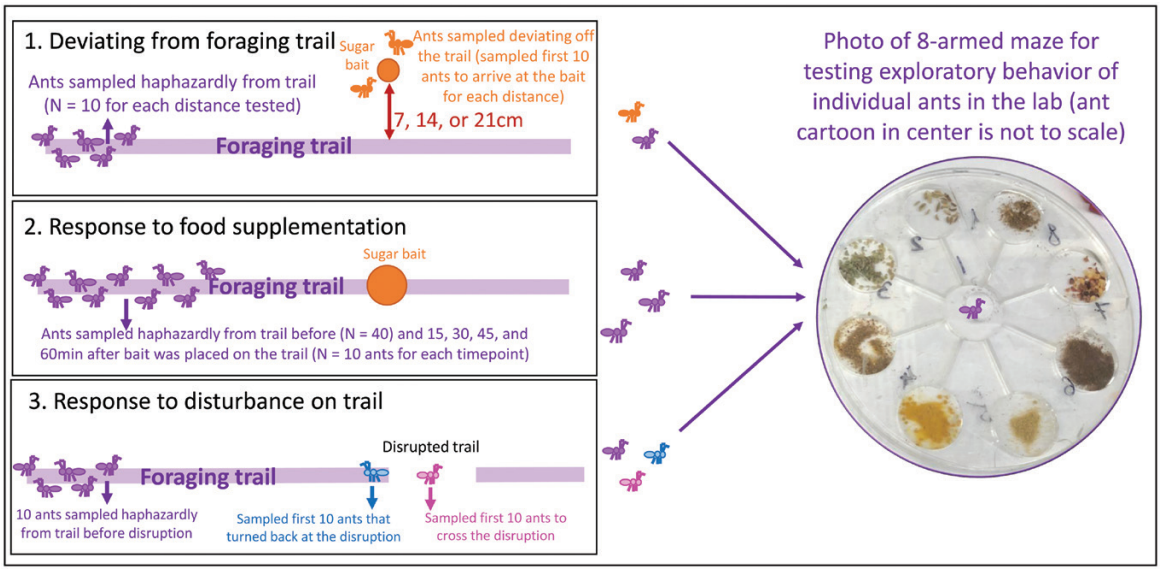

Figure 1. Experimental procedure for testing the three different hypotheses. The three boxes on the left detail the sampling procedure for each experiment in the field. On the right is a photo of the 8-armed radial maze in which sampled ants were tested for exploratory behavior in the lab.

Data analysis

To examine whether ants that deviate from the foraging trail are more exploratory than ants on the foraging trail and whether the distance of the bait affects exploratory behavior , we used a Generalized Linear Model (GLM) with a Poisson link function for count data. In the GLM, the number of visits an ant made to the arms of the 8-armed maze was the response variable. The two explanatory variables in the model were whether the ant was collected on or off the trail, and the distance of the bait from the trail (7, 14, or 21 cm). To determine whether food supplementation on a foraging trail influenced the proportion of exploratory individuals on the foraging trail, we ran 2 separate GLMs with a Poisson link function for count data. One model tested whether trail rate changed over time and the other tested whether exploratory behavior changed over time. In both statistical models, time was the explanatory variable, and either exploratory behavior (number of visits to spices) or trail rate (number of ants walking on the trail in 30 s) was the response variable. Finally, to test whether ants that crossed a disruption in the foraging trail were more exploratory than the mean forager population or than ants that turned back when faced with the disturbance, we ran a GLM. Exploratory behavior was the response variable and whether ants were collected before the disturbance, crossed the disturbance, or turned back at the disturbance, was the explanatory variable in the GLM. All analyses were conducted in R version 4.1.1 (R core team 2021), using the Anova() function from the package "car" (Fox and Weisberg 2018) to report analysis of deviance. Code and data are available as Supplementary Materials.

Results

We found support for our first hypothesis that ants that deviate from the foraging trail are more exploratory than those that do not. Furthermore, we found that in line with our second hypothesis, food bait on a foraging trail effectively increased the proportion of exploratory individuals on a trail. However, we did not find support for our third hypothesis that the first responders to a disturbance on the trail would be more exploratory than non-responders.

Deviating from foraging trail

Ants that deviated from the foraging trail were more exploratory than ants that conformed to the foraging trail. The exploratory behavior tested in the lab of ants that deviated from the trail was statistically significantly greater than the exploratory behavior of ants collected from the foraging trail itself (GLM: on/off trail: χ^2= 14.007, df = 1, P < 0.0002, Figure 2A). However, the distance of the bait from the trail did not impact the exploratory behavior of the ants (GLM: distance of bait: χ^2 = 4.584, df = 2, P = 0.101, Figure 2B)

Response to food supplementation

The proportion of exploratory individuals on the trail increased over time after adding food on the trail. We found that trail rate decreased over time after the food supplement was provided (GLM: χ^2 = 8.93, df = 1, P = 0.0028, Figure 3A) but the exploratory behavior of the ants on the trail did not change following food supplementation (GLM: χ^2 = 2.725, df = 1, P = 0.099, Figure 3B). Thus, because there was a reduction in the number of ants on the trail over time and no change in

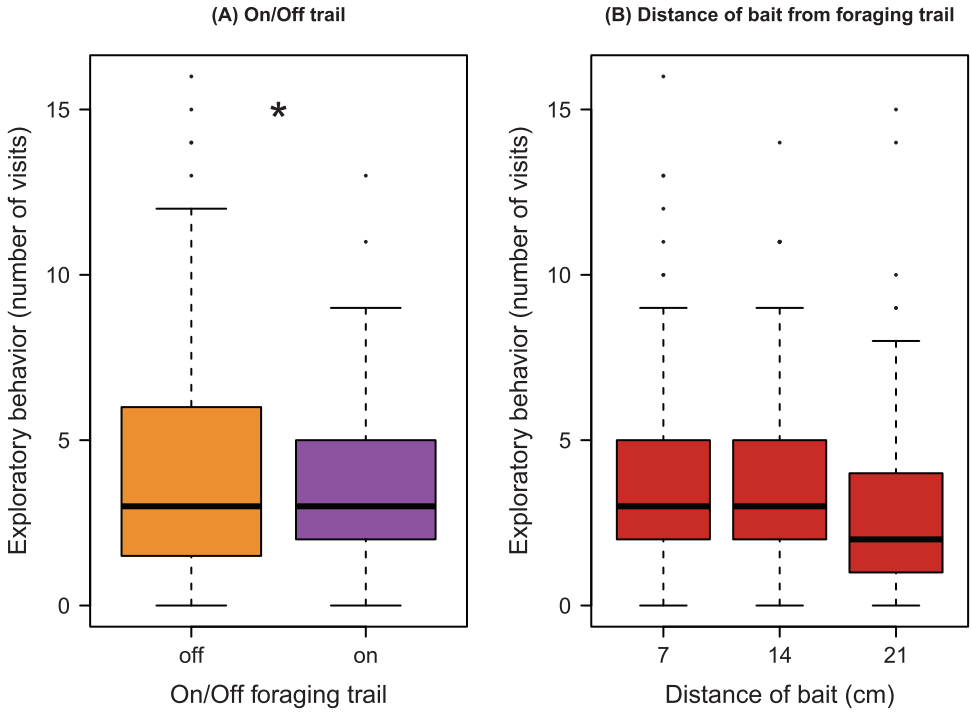

Figure 2. Exploratory behavior in relation to deviating from the foraging trail. Exploratory behavior of individual ants (number of visits to arms in an 8-armed maze in the lab) was greater (A) for ants that deviated from the foraging trail (off trail, orange) for all bait distances (N = 160 ants, N = 6 trails), than for ants that were collected from the foraging trail (on trail, purple) (N = 160 ants, N = 6 trails). However, (B) exploratory behavior did not relate to the distance of the bait from the foraging trail (7 cm [N = 120 ants, N = 6 trails], 14 cm [N = 100 ants, N = 5 trails], and 21 cm [N = 100 ants, N = 5 trails]). Here and in all following box plots, horizontal lines are the medians, boxes extend to 25 and 75 percentile, whiskers extend to 1.5 times the interquartile range, and dots are outliers. Asterisk indicates statistical significance (P < 0.0002) with a GLM.

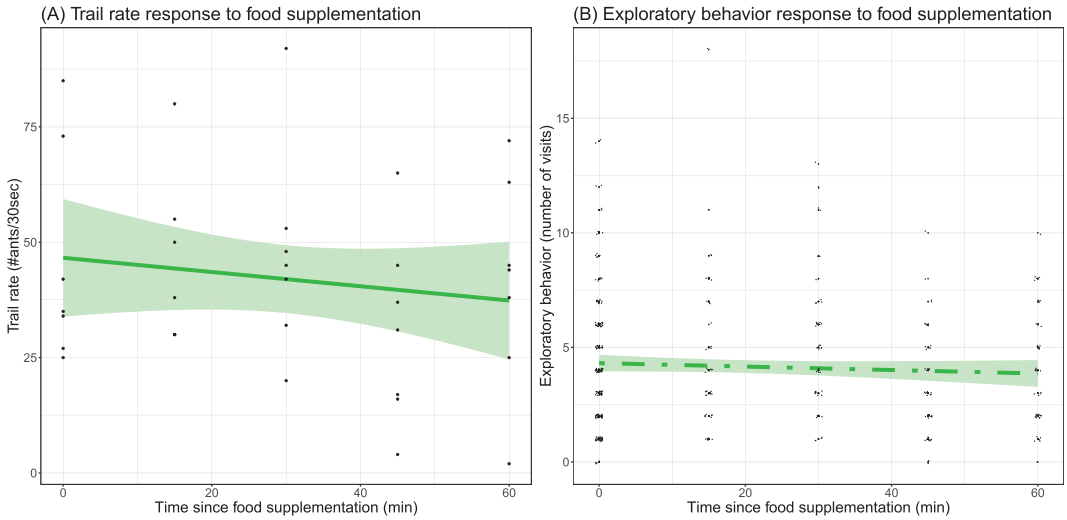

Figure 3. Trail rate and exploratory behavior after food supplementation. (A) Trail rate decreased over time (measured every 15 min) after food supplementation (N = 7 trails). (B) Exploratory behavior of ants collected after food supplementation did not change (N = 400 ants). Points are slightly jittered along the x- and y-axis to enhance visibility, the lines are linear fits to the data with 95% confidence interval (shaded area around the lines) plotted using the geom_smooth() function in the 'ggplot2' package of R, with the default Loess method. Solid line (A) indicates a statistically significant relationship and dashed line (B) a non-significant relationship from a GLM.

the exploratory behavior of the individuals collected from the trail, exploratory behavior effectively increased after supplementing the foraging trail with food. The reduction of ants on the trail can be attributed to an accumulation of ants at the bait, and our data suggest that the ants that accumulate at the bait are the non-exploratory individuals.

Response to disturbance on trail

We did not find that exploratory individuals facilitated reestablishing a disturbed foraging trail. We did not detect a statistically significant difference in exploratory behavior of ants that were collected before the trail disturbance, ants that were first to cross the disturbed area of the trail, and ants that turned around when they reached the disturbed portion of the trail (GLM: disturbance state: χ^2 = 0.109, df = 2, P = 0.947, Figure 4).

Discussion

We found that exploratory individuals are allocated to where they are most needed in the context of recruitment to new food and changes to existing food resources, but not in response to disturbance. Individuals that veered off the main foraging trail were more exploratory than individuals that kept to the trail (Figure 2A) regardless of the distance of the food bait from the foraging trail (Figure 2B). Furthermore, the proportion of exploratory individuals on the foraging trail increased in response to adding food to the foraging trail—the trail rate decreased over time (Figure 3A) and the average exploratory behavior of sampled individuals persisted (Figure 3B). Lastly, we did not find evidence that an ant's response to a disturbance on a foraging trail is related to its exploratory behavior (Figure 4).

Colonies of *L. humile* seem to allocate exploratory individuals to the discovery of new food sources. Ants that were collected from off the trail were more exploratory than those that were collected from an established foraging trail (Figure 2A). This result is especially compelling because ants sampled from the main foraging trail likely included both individuals that would not veer off the trail as well as individuals that might deviate from the trail later. If we had a way to distinguish the two types of individuals when sampling from the main trail and collect only ants that conform to the foraging trail, we might have seen a larger effect size. Contrary to our predictions, we found that the distance an ant veered off the trail did not relate to its exploratory behavior (Figure 2B). Individuals that veer off from the main foraging trail can form new recruitment trails to novel foods (Flanagan et al. 2013). Our work shows that behavioral differences among individuals may determine which ants instigate these new trails—the ones that are most exploratory. Previous work showed that exploratory behavior in *L. humile* is persistent for at least a few days and is linked to the expression of the *Lhfor* gene (Page et al. 2018). Thus, in the timeframe of our experiments, exploratory behavior was likely a persistent trait. Future work might uncover further proximate mechanisms that underlie exploratory behavior in *L. humile* workers and determine the duration of its persistence. While it might seem surprising that there was no relationship between how far an ant veered off from the trail and its exploratory behavior, it is possible that high exploratory behavior is simply a switch for leaving an established trail. However, if it is not a switch, examining more and farther bait distances will reveal the relationship between exploratory behavior and bait distance. Linking lab quantification of exploration to the ecological meaning of the behavior (Mouchet and Dingemanse 2021) is important for our understanding of individual variation in exploration.

Exploratory behavior was linked to the exploitation of a known food source. Our experimental manipulation of adding food to the trail led to an increase in the proportion of exploratory individuals. The trail rate decreased while the exploratory behavior of individuals sampled from the trail did not change after adding food. Thus, the proportion of exploratory behavior increased. It is possible that because exploratory behavior is often linked with recruitment behavior in social insects (Lemanski et al. 2019), adding a food source to the foraging trail required the recruitment of new ants to the added food. In contrast, in established trails that are not

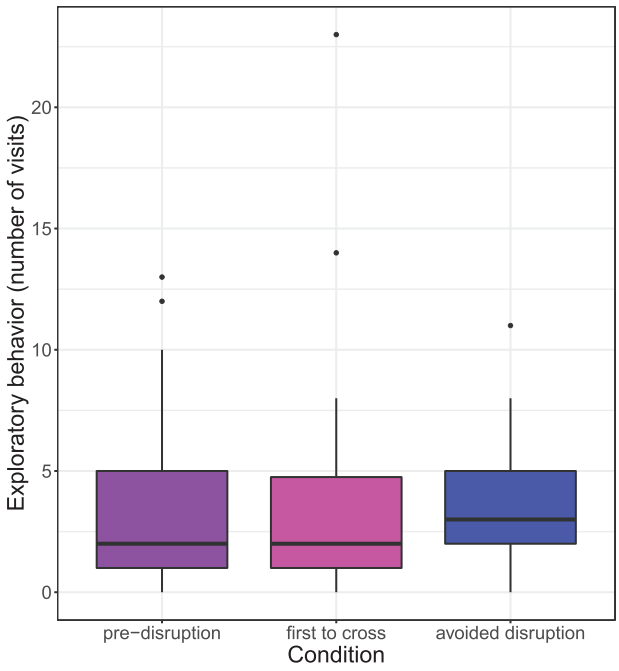

Figure 4. Exploratory behavior in response to disruption on the foraging trail. Ants collected before the trail was disrupted are referred to as "pre-disruption" (purple) (N = 70 ants, N = 5 trails), ants that were the first to cross the midpoint of the disrupted area are referred to as "first to cross" (pink) (N = 70 ants, N = 5 trails), and ants that turned around when they reached the disrupted portion of the trail are referred to as "avoided disruption" (blue) (N = 70 ants, N = 5 trails).

manipulated (like those examined by Page et al. [2018]), the proportion of exploratory behavior is at a steady state that is linked to the amount of food the trail leads to. Future studies may examine whether supplementing low-use trails results in a more prominent increase in the proportion of recruiting exploratory individuals relative to the increase in exploration we found on high-use trails.

Finally, we did not find a relationship between exploratory behavior and response to disruptions while foraging. Ants that crossed a disturbed area did not differ significantly in their exploratory behavior from ants that did not cross a disturbed area (Figure 4). It is possible that behaviors other than exploration relate to the propensity of an individual to cross a disturbed area. For example, Verbeek et al. (1994) showed that moving into a novel environment is related with boldness/risk taking in great tits. While previous work has linked exploratory behavior with risk taking (Verbeek et al. 1994; Fraser et al. 2001; Wilson and Godin 2009), we did not find such a link. It is possible that our perturbation did not reflect naturally caused disturbances. Future work could examine different ways for quantifying risk-taking behavior in the field and lab to determine whether "risky" individuals are allocated to particular tasks, just like exploratory individuals.

Understanding the ecological consequences of individual differences in behavior on the collective behavior of social animals may bring us closer to understanding the causes of these consistent individual differences. Our work shows that exploratory individuals are allocated to where they can best facilitate the collective foraging of ant colonies. It is possible that individuals that exhibit other behavioral types (like boldness or risk taking) are allocated differentially to where those behaviors are most beneficial for the colony. Uncovering when certain individuals are allocated to particular tasks and which behavioral types facilitate different collective behaviors is fundamental for understanding social organization. More broadly, our work highlights the importance of considering both ecological and social contexts when examining different types of behaviors.

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Author Contributions

MM conceived the study and performed all the experiments. MM and NPW designed the experiments, analyzed the data, and wrote the manuscript jointly.

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Data Availability Statement

All data and analysis code are available as Supplementary Materials. All data generated and analyzed during this study are included in this published article and its supplementary information files.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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