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RESEARCH ARTICLE

Ant foraging path use responds to different types of risk and their encounter probabilities

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Abstract

Ant colonies are likely able to access food locations by multiple paths that can vary predictably in length or mortality risk. To favor one path over another requires ants to perceive, communicate and act upon important differences in length and risk between paths. Here, we present replicate *Linepithema humile* colonies with four equal-length paths to a sugar source. The paths vary in probabilities of encountering a risk cue that range from 0 to 100%. The risk cues were either live workers of an aggressive competitor (*Liometopum occidentale*: LO) or only formic acid (FA), a defensive chemical common in many formicine species. Both the probabilities of encounter and type of cue affected path preferences. Although across both cues the zero-risk path was most used, the use was not exclusive and patterns of response to the cues differed significantly. More ants were on all the paths when the cue was LO rather than FA, leading to a higher success rate at finding food. Worker numbers on paths with LO did decline over time as consistent with recognizing neighbors to be 'dear enemies' that are a reduced threat to the colony. Similarly, changes in path usage suggested that the FA cue also became viewed as less threatening over time when competitors were never simultaneously present. The results are consistent with *L. humile* exhibiting the behavioral plasticity and communicative ability needed to categorize and predict risk to efficiently collect food while defending against other ant species.

Keywords Ants · Foraging · *Linepithema* · Risk · Perception · Communication

Introduction

A potential advantage for group foraging species such as ants is the ability to gather information across spatially separate locations at the same time. For example, colonies can compare separate food patches simultaneously in terms of food quality and predation risk, and thereafter bias exploitation towards the more advantageous (Nonacs and Dill 1988, 1990, 1991; Tanner 2008). Such effective decision-making depends on accurate communication, however, and not all information is shareable in the same way. Thus, an ant can directly experience the quality of a food source through trophallaxis with returning foragers without leaving its nest. In contrast, to inform others about dangers on a path to a food source a forager needs to be able to communicate about an unshared experience (Nonacs 1990).

Besides finding dispersed food sources at the same time, multiple foraging ants can also simultaneously explore alternative pathways to a single food source. This strategy can maximize food collection rates by finding the shortest or straightest path between the food and the nest (Beckers et al. 1990; Yates and Nonacs 2016; Latty et al. 2017), or stationing workers on the path for rapid recruitment (Denton and Nonacs 2018). Additionally, if mortality risk appears on a particular route to a food location, multiple foragers could efficiently communicate alternative and safer pathways to use.

Unlike the physical length or straightness of a path, mortality risk on a path to a food source can vary across time (Nonacs and Dill 1991). Therefore, foraging ants may need to continuously sample various routes to measure both the current conditions and to develop expectations about the possibility of future dangerous encounters (Stephens and Krebs 1986). Combining older information with newer information to alter expectations (i.e., Bayesian updating:

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Valone 2006) occurs in a wide variety of taxonomic groups (e.g. Lima 1984, 1985; Valone and Brown 1989; Valone 1991, 1992; Krebs and Inman 1992; Alonso et al. 1995; Olsson et al. 1999; van Gils et al. 2003; Stamps et al. 2018), including ants (Nonacs and Soriano 1998).

In this study, we present colonies of Argentine ants (*Linepithema humile*) with access to four alternative paths of equal length to a single food source. The paths differ only in the types of negative stimuli encountered and the frequency of encountering the stimuli, ranging from 0 (never present) to 100% (always present). The negative stimuli are either live aggressive *Liometopum occidentale* workers (LO) or formic acid (FA), a defensive chemical common in many formicine species. Both *Lio. occidentale* and *L. humile* have similar sociobiology in establishing dense foraging trails and being highly aggressive towards other species at food sources (Ward 1987). However, *L. humile* can invade natural habitats of *Lio. occidentale* and are observed to eventually aggressively exclude them (Ward 1987; Menke et al. 2018). Formic acid is an effective chemical weapon in formicine ant species. For example, in *Nylanderia fulva* their use of formic acid appears to be the key to competitive dominance in combat with the myrmicine, *Solenopsis invicta* (LeBrun et al. 2014). Therefore, our experiment tests: (1) the degree to which ant foragers respond and adjust their path usage to different probabilities of encountering stimuli suggestive of a mortality risk, and (2) whether or not ants differentially respond to situation-specific cues of mortality risk.

Methods

Collection

Six replicate colonies of *L. humile* containing approximately 500–800 workers, 6–8 queens, and brood were collected on the campus of the University of California, Los Angeles. Colonies were collected from a minimum of 250 to a maximum of 1250 m apart to avoid collecting ants from the same 'colony' as defined by Heller et al. (2008). The ants were nested in open plastic containers (sides coated with Fluon) and filled with molded plaster of Paris kept moist for humidity. Water was provided ad libitum. Colonies were examined every 4–5 days and workers were added if numbers obviously dropped below 500. Added workers always came from the same site as the original group.

Experiment

The experimental arenas (Fig. 1) consisted of four equal length (90 cm) paths made of clear, plastic tubing to a single foraging arena. A container with sugar water was placed in the foraging arena (Fig. 1—arena labeled "Food") daily between approximately 12:00 and 15:00 h. Time until the first ant found the food was recorded up to the first 10 min. Food was removed 2 h after placement (whether or not ants were foraging), to avoid colonies becoming satiated.

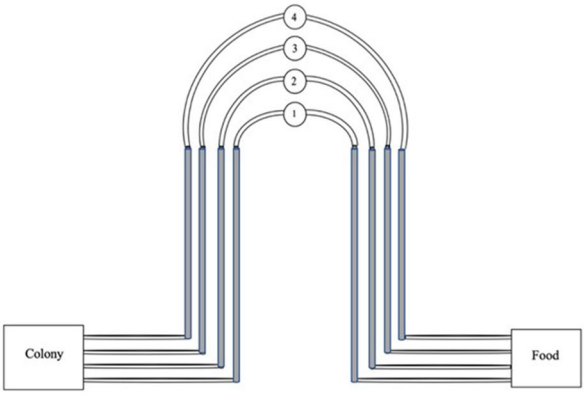

Fig. 1 Schematic diagram of the experimental foraging arena. Containers labeled 1–4 indicated where negative stimuli were placed. Although differing in the illustration, all paths were of equal length in the experiment

To use three of the four paths, foragers had to potentially pass a negative stimulus in an arena at the midway point of each path (Fig. 1; Supplement Figs. 1, 2). The stimulus was either several workers of the aggressive velvety tree ant (*Lio. occidentale*: LO, Hoey-Chamberlain et al. 2013) or formic acid (FA). The stimuli were placed along paths between 8:00 and 11:00 h daily and remained for approximately 24 h. The four paths differed such that either FA or LO was never (0%) or always present (100%), or appeared randomly, but on average, every fourth (25%) or second (50%) day. Across the colonies, the order of the risk level on the paths was varied (e.g., Path #1 could range from never to always risky for a given colony). Each *L. humile* colony participated in enough trials to experience the negative stimulus at least four times on the 25% path. Thus, for any given trial, a range of 1–3 paths would have FA or LO present.

The *Lio. occidentale* were collected from Descanso Gardens (Los Angeles, CA) and housed similarly to the *L. humile*. Both *L. humile* and *Lio. occidentale* are in the same subfamily of Dolichoderinae. FA is the primary defensive chemical used by ant species in the subfamily Formicinae (Hefetz and Blum 1978; Blum 1978).

Risk cue: FA

For a given colony, cotton pads with 100 µL of FA could be placed in three of the four arenas according to the above predetermined frequency of risk and presentation schedule (Fig. 1). The quantity of FA was determined based on preliminary experiments varying the amount of FA and measuring its effect on *L. humile*. Furthermore, the arenas had

lids with small holes that prevented the FA from entirely dissipating or accumulating in amounts lethal to *L. humile*. If FA was to be absent the next day, the arenas were cleaned to remove any leftover traces.

Risk cue: LO

Approximately 15–20 LO workers were placed in arenas relative to the predetermined frequency of risk and presentation schedule. Mesh barriers prevented direct contact and fighting with the *L. humile* workers. However, they were able to exchange chemical cues. LO workers were removed and replaced daily to ensure their numbers and effect were consistent. If LO were to be absent the next day, the arenas were cleaned to remove any leftover traces.

Video observations

Webcams recorded 15 min of path use, up to three times per day: one at least 3 h 'before' food presentation, one 'during' food presence, and one at least 3 h 'after' food had been removed.

Video scoring

Only the number of ants crossing a section of the paths (e.g., shaded portion shown in Fig. 1) were scored across the 15-min time period. Observers kept spatial track of a forager's location on the video to avoid double-counting an ant moving back and forth on the same path.

Statistics

Three replicate colonies experienced only the FA risk cue treatment and three more experienced only the LO treatment. The effects of each treatment were analyzed separately by four-factor ANOVAs. The dependent variable was the number of ants observed on each of the four paths (ln-transformed) in a trial. The independent variables were: path (the routes with 0, 25, 50 or 100% probability of having the risk cue); food (observations taken 2 h before sugar water was made available, during the period the sugar water was available, or 2 h after removal); danger level (during the observation, did 1, 2 or 3 paths have a risk cue present); and time (the sequence of trials in the experiment divided into four quartiles of experimental days 1–6, 7–12, 13–18, or > 18). Days were aggregated into quartiles, because the number of observations across colonies varied as some had to be discarded due to ants escaping or clarity issues with videos. The number of days a given colony experienced trials ranged from 21 to 27 (mean = 23.67). When main effects of the independent variables were significant, we tested for significant differences across the levels of the variables through Scheffe post hoc tests.

For a comparison across the type of risk cues, we used the mean number of ants per day on each path across the four trial quartiles as the dependent variable in an ANOVA with type of cue, path and quartile as the independent variables.

Linear-mixed effect models analyzed the amount of time ants took to find food based on trial sequence and treatment type (FA or LO) all in R version 3.5.2 (R Core Team 2018). First, a null model contained only the colony as a random intercept. Then, iteratively fixed effects were incorporated to find the combination with the lowest AIC value. We conducted an ANOVA to examine the mean time to find food across days by stimulus type (FA or LO).

Results

In comparing across risk treatments, significantly more workers were on all the paths in the LO treatment relative to the FA treatment (Fig. 2, the all series of bars: $F_{1,73} = 24.92$, $p < 0.0001$). Colonies distributed their workers significantly differently across the four paths of risk ($F_{3,73} = 3.303$,

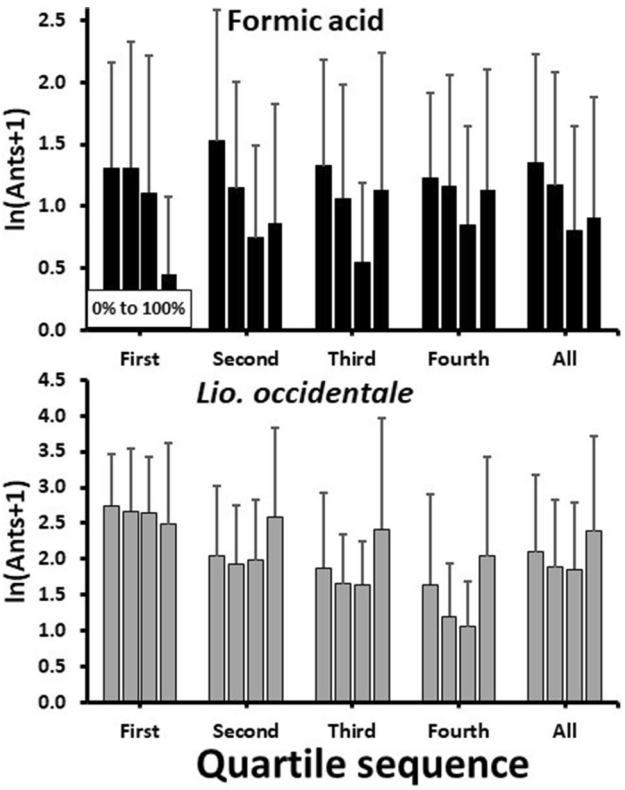

Fig. 2 Mean number (± SD) of ants per day on each on the four paths by time series quartiles or across the entire experiment. The risk cues (formic acid: FA, or *Lio. occidentale* workers: LO) were either never present on a given path or present on 25, 50 or 100% of the days

$p = 0.0248$), and the interaction between risk type and path use was marginally significant ($F_{3,73} = 2.717$, $p = 0.0508$). Overall, the ants were observed more often on the 0 and 100% paths, and particularly so when the cue was LO (Fig. 2, the all series of bars). Time, in terms of quartile sequence, did not have a significant effect ($F_{3,73} = 1.025$, $p = 0.3865$). No other higher interaction terms were significant ($p > 0.3$).

In examining only the FA treatment (Table 1), worker numbers significantly differed across the four paths. Scheffe post hoc test grouped paths 0 and 25% as significantly more used than paths 50 and 100% (Fig. 3). Worker presence was significantly affected by the appearance of food. For this main effect, the Scheffe test found that there were significantly fewer ants on the paths before the food appeared than while it was present and after it was removed. Neither the main effect of trail sequence as quartiles nor the number of paths with a risk cue in a trial was significant. However, trial sequence did have significant interactions with both paths and food, with worker presence on the riskier paths increasing over time (Fig. 2: first through fourth quartile series of bars; Table 1).

In examining only the LO treatment (Table 1), worker numbers significantly differed across the four paths. Scheffe post hoc test grouped the 100% path as having significantly more ants on it than on Paths 25 and 50% (which were not significantly different from each other: Fig. 3). Path 0% was intermediate in usage and significantly more or less used than the other three paths. Worker presence was also significantly affected by the appearance of food. By Scheffe test, there were significantly fewer ants on the paths before the food appeared than while it was present (Fig. 3). The mean number of ants on paths after the food was removed was intermediate to before and during, but significantly different from either. Trial sequence had a significant effect (Fig. 2: first through fourth quartile series of bars; Table 1), with Scheffe tests finding that there were significantly fewer ants across all the paths in each subsequent quartile, except between the second and third quartiles (Fig. 3). Trial sequence also produced a significant interaction with path usage, such that colonies concentrated proportionally more worker activity into the 0 and 100% paths as the experiment progressed (Fig. 2). I.e., the decline in path usage was most pronounced on those with the more intermediate occurrence of risk cues.

For examining time to find food across days, including stimulus type as a fixed effect significantly improved model fit (Table 2). This indicates that food was found significantly faster in LO treatments than in FA treatments (Fig. 4; $p < 0.0001$). Across trials, for both stimulus types, there was a trend to find the food faster, but neither decrease was statistically significant (Fig. 4).

Table 1 ANOVA results

Variable	df	F	A	L	O
		F	*p*	*F*	*p*
Path	3	**10.018**	**< 0.0001**	**7.567**	**< 0.0001**
Food	2	**4.634**	**0.0101**	**7.298**	**0.0007**
Danger	2	1.615	0.1997	0.573	0.5640
Time	3	1.555	0.1992	**22.087**	**< 0.0001**
P×F	6	0.858	0.5255	0.887	0.5044
P×D	6	0.546	0.7730	0.334	0.9192
P×T	9	**2.869**	**0.0025**	**2.339**	**0.0136**
F×D	4	1.046	0.3827	0.272	0.8926
F×T	6	**2.677**	**0.0143**	0.514	0.7979
D×T	6	1.973	0.0676	1.004	0.4215
Residual	596/556				

Paths are where risk cue is present in 0, 25, 50 or 100% of trials. Food are observations before, during and after the addition of sugar water. Danger is the number of paths (1–3) that had a risk cue during a trial. Time is first through fourth quartile of trials that colonies experienced. The residual df's are given for the FA and LO treatments, respectively. All interactions greater than pairwise between the variables were non-significant and not shown

FA formic acid as risk cue, *LO Lio. occidentale* as risk cue

Discussion

Argentine ant colonies clearly evaluate and communicate about the properties of pathways to a food source. Their overall responses further indicate flexibility in balancing multiple objectives and different types of risk. Colonies could have avoided all risk exposure by only using the one path that was always safe and ignoring the other three, but this was not the case. Although the safest path was the most used, there also remained significant traffic on the paths with risk cues present from 25 to 100% of the time (Fig. 2). This response is significantly different from *Lasius pallitarsis* in which risky paths and patches were strongly avoided when there was no cost in terms of food gain (Nonacs and Dill 1988). As an aggressive invasive species, this suggests that for *L. humile* area defense and foraging are complimentary activities (Holway 1999; Holway and Case 2000) where to efficiently exploit food resources, competing species need to be excluded.

The strategy used by *L. humile* provides insight into how other aggressive, dominant organisms may be balancing these competing demands. In particular, this study provides a behavioral assay that can be performed to determine how space use varies across organisms indicating where they fall on the bold versus shy or dominant versus subordinate axis.

The different types of risk also elicited different responses. In nature, Argentine ants are intensely aggressive towards and with *Lio. occidentale* colonies (Ward

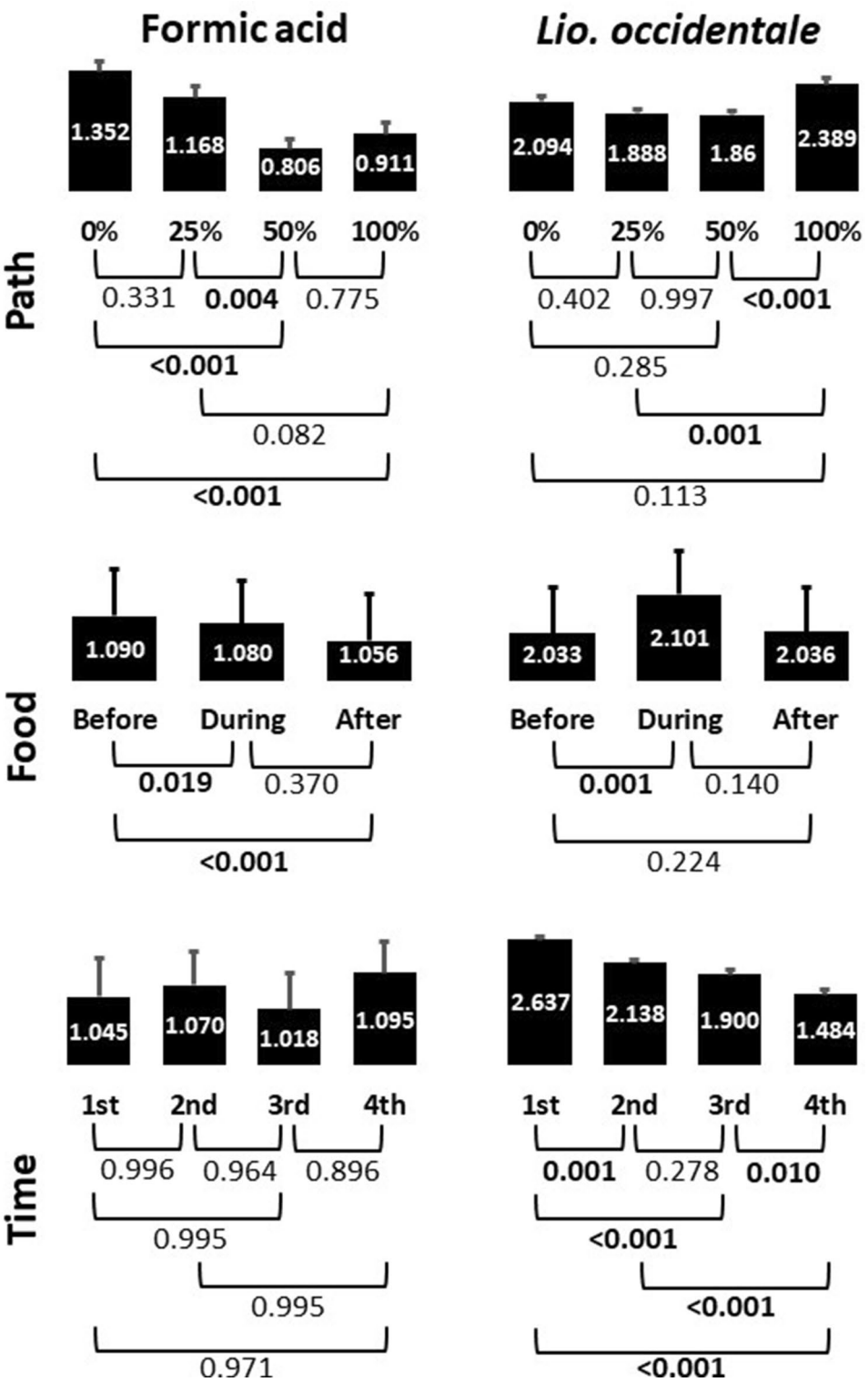

Fig. 3 Scheffe post hoc tests on the significant main effects from the ANOVAs. Histograms show the means (ln transformed and with S.E.) of the levels of the variables. Brackets show the comparison tests and their level of significance

1987; Menke et al. 2018). Thus, the presence of live *Lio. occidentale* workers in our experiments may account for why Argentine ants patrol or defend the paths more intensely than in response to only formic acid. This effect might be attributed to the effectiveness in formicine species of FA as a chemical weapon such that its presence of FA may favor Argentine ants becoming more likely to avoid these paths. Interestingly, however, worker ant presence on the riskiest FA path did increase over time (Fig. 2). Thus, it appears that the repellent effect declines when never paired with any actual encounters with a competing species. This would suggest a Bayesian feedback

Table 2 Model comparison for time data across days

Model name	AIC	Model formula	Comparison	Results	*p*
m0	268.7	ln_Time ~ (1|Colony)	N/A	N/A	N/A
m1	269.0	ln_Time ~ Day + (1|Colony)	m1, m0	Not significant	0.1919
m2	260.4	ln_Time ~ Day + Stimulus + (1|Colony)	m2, m1	Significant	0.0011

Model m2 was chosen based on AIC value and comparison with other models using likelihood ratio tests

process that does evaluate a signal of risk in terms of its accuracy in truly predicting mortality rates.

Alternative to avoiding FA areas, the results might indicate that live *Lio. occidentale* attract more workers. Although the design prevented actual fighting, some physical contact was possible through the mesh. Actual contact with aggressive heterospecifics may, therefore, have stimulated a defensive reaction as seen in the consistently higher number of workers on the 100% risky path (Figs. 2, 3). Over trials, a different Bayesian process than observed with FA seems to be occurring: the numbers of defending workers decrease over time across all the paths (Fig. 3), and especially on those that either never or only sometimes have risk present (Fig. 2). This would be consistent with learning that a neighbor is a 'dear enemy' and not an imminent threat to the colony (Langen et al. 2000). The 'dear enemy' effect (Fisher 1954; Jaegar 1981), therefore, results in a decrease in aggressive behavior towards familiar neighbors. The dear enemy effect has been demonstrated in a wide variety of taxa (Temeles 1994; Booksmythe et al. 2010) including other species of ants, fiddler crabs and cichlid fish (Langen et al. 2000; Detto et al. 2010; Weitekamp and Hofmann 2017).

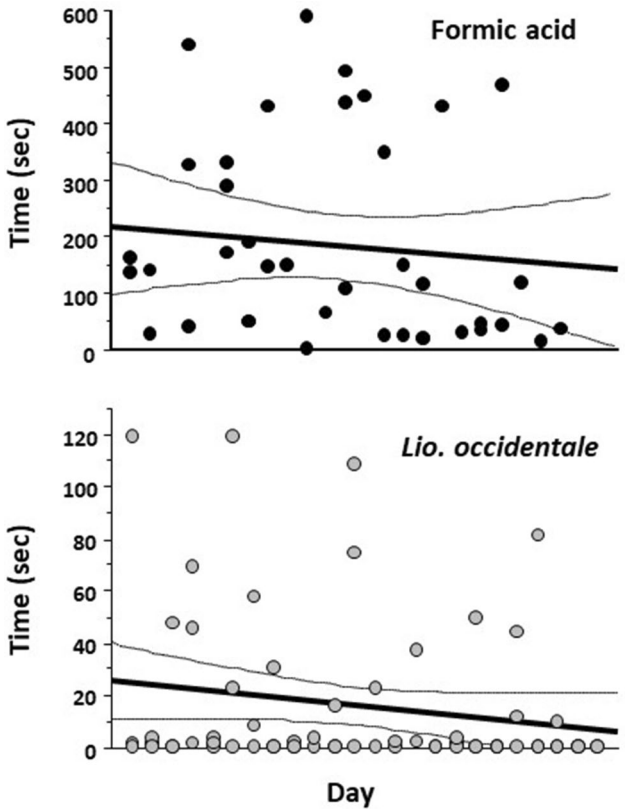

Fig. 4 Time to find food by colony across days of the experiment, with overall trend lines and 95% confidence intervals. Neither the FA ($F_{1,40}=0.476$, $p=0.494$) or LO ($F_{1,64}=2.321$, $p=0.133$) regressions of time by day were significant. Trials in which colonies failed to find the food within 600 s were excluded from analyses

The large numerical difference in response to LO versus FA (independent of if it resulted from avoiding FA or attraction to LO) resulted in LO colonies finding food significantly faster. This suggests that food discovery rate by Argentine ants can be directly affected by their responses to encountering different competitive species.

How ant species respond to the presence of other ant species near their nest and possibly on routes to food sources may provide insights into how they integrate within ant communities. The observed behavior of *L. humile* is consistent with dominating space: workers were found on all the paths to the food, using safe paths to access food, but also 'defending' their space by their more numerous presence on paths with heterospecific cues. In similar foraging versus risk trade off trials, other species show very different responses. *L. pallitarsis* colonies will avoid risky paths if safe paths of equal length are available (Nonacs and Dill 1988) and only take mortality risks for significantly better food resources (Nonacs and Dill 1990). *Myrmica incompleta* colonies, however, will often ignore the food to instead concentrate on attacking a heterospecific intruder, even if such behavior can result in catastrophic casualties to the worker population (Nonacs 1988). It would be interesting to examine if such differences in controlled foraging trials predict species–species interactions in nature and physical distribution in communities. For example, the success of Argentine ants as an invasive species is attributed to their efficiency in finding food (e.g., dominating space) and their extreme and successful aggression towards competing species (Ward 1987; Holway 1999; Holway and Case 2000; Menke et al. 2018). This study further demonstrates the flexibility of their communication networks to local conditions in being able to respond differently across types of threats and adjust those responses over time.

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Author contributions EKL and PN both conceived the experiment and the design. EKL collected and maintained the ants, and supervised and collected the data. EKL and PN jointly analyzed the data and wrote the manuscript.

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Data availability Data will be deposited in Dryad upon acceptance.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Consent for publication Granted, the material in the manuscript has not been published and is not in submission at any other journal.

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