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The value of spatial experience and group size for ant colonies in direct competition

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Abstract Animals often search for food more efficiently with experience. However, the contribution of experience to foraging success under direct competition has rarely been examined. Here we used colonies of an individually foraging desert ant to investigate the value of spatial experience. First, we trained worker groups of equal numbers to solve either a complex or a simple maze. We then tested pairs of both groups against one another in reaching a food reward. This task required solving the same complex maze that one of the groups had been trained in, to determine which group would exploit better the food reward. The worker groups previously trained in the complex mazes reached the food reward faster and more of these workers fed on the food than those trained in simple mazes, but only in the intermediate size group. To determine the relative importance of group size versus spatial experience in exploiting food patches, we then tested smaller trained worker groups against larger untrained ones. The larger groups outcompeted the smaller ones, despite the latter's advantage of spatial experience. The contribution of spatial experience, as found here, appears to be small, and depends on group size: an advantage of a few workers of the untrained group over the trained group negates its benefits.

Key words *Cataglyphis*; colony size; dominance-discovery trade-off; learning; maze solving; social insects

Introduction

Competition, that is, the negative effect of one organism on the fitness of another by either depleting shared resources or preventing access, is a fundamental phenomenon in ecology and evolution that often affects diverse phenotypic traits of the interacting species, for example by character displacement (Mitchell *et al.*, 1990; Gurevitch *et al.*, 1992; Keddy, 2001; Bolnick, 2004; Grant & Grant, 2006). Intraspecific competition is usu-

ally stronger than interspecific competition because the niches of individuals of the same species overlap more than those of individuals of different species (Adler *et al.*, 2018). Competition indeed intensifies with the similarity in the ecological niche of the competitors and with increasing densities (Abrams, 1975; Mesz  na *et al.*, 2006). There are however several mechanisms that facilitate coexistence either within or between species, such as niche broadening and segregation in time, space, or diet (Bolnick, 2001; Perrin & Kotler, 2005; Svanb  ck & Bolnick, 2007).

Some individuals or species are stronger competitors than others, dominating resources and preventing others from accessing them (Steinwascher, 1978; Charter *et al.*, 2013). Inferior competitors must therefore rely on other strategies, such as better dispersal capabilities

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(Zirkle *et al.*, 1988; Bolin *et al.*, 2018). In ants, a trade-off between food discovery and dominance can be found in many communities, with some species discovering food more quickly, while others arrive later but are then able to dominate the resources (Fellers, 1987; Perfecto & Vandermeer, 2011; Cerdá *et al.*, 2013; Tiong & Morse, 2021). A similar trade-off is that of exploration vs. exploitation, in which some species discover resources faster while others exploit them more thoroughly (Schmitt, 1996; Monk *et al.*, 2018). Such a trade-off can occur among colonies of the same species but of different sizes or with different behavioral characteristics and can pertain also to targets other than food resources (Hills *et al.*, 2015; Katz & Naug, 2015; Kembro *et al.*, 2019).

Foraging for food, which in many species improves with experience, is a vital behavior with direct consequences for reproduction and survival. In ants, a recent successful foraging event, for example, can increase the likelihood of the ants leaving their nests and foraging again (Robinson *et al.*, 2012; Gilad *et al.*, 2022a). Foraging also improves with increasing spatial familiarity with the habitat, which assists in exploration and food discovery (Dukas & Real, 1993; Wolf, 2008). Central-place foragers, such as social insects, nesting birds, and burrow-dwelling rodents, leave the nest/burrow to forage and then return to it (Orians & Pearson, 1979; Ydenberg *et al.*, 1986). For these animals, experience should play a particularly important role in foraging, especially when it is profitable to revisit patches that have not been fully depleted. Such experience should be expressed in faster arrival at the food patch and return to the nest (Dyer, 1998; VanderSal, 2008). As central-place foragers, ants benefit from foraging experience through the increased likelihood of discovering food and increased speed of return to the nest and handling the food (Johnson, 1991; Chameron *et al.*, 1998; Saar *et al.*, 2020).

Competition is common and strong both within and between ant species (Heinze *et al.*, 1996; Parr & Gibb, 2010; Cerdá *et al.*, 2013; Erős *et al.*, 2020). The competition outcome can be influenced by colony size, with larger colonies dominating smaller ones (Palmer, 2004; Tanner, 2006; see also McGlynn, 2000, for a more complex pattern, depending also on interaction type). The role of spatial experience in direct intraspecific competition among ant colonies has never been examined, and colony size may interact with experience to affect competition over food.

Our aim here was to determine whether spatial experience can provide an advantage in direct intraspecific competition for food between groups of ant workers. Our model was the individually foraging desert ant, *Cataglyphis niger*, searching for food in a laboratory

maze. Our goal was to employ a laboratory design that would be challenging for the ants, and in which spatial learning might play a role, rather than to imitate the natural conditions. We have demonstrated previously in a series of laboratory experiments that *C. niger* ants improve with experience in solving a maze and that the improvement is based on a combination of spatial learning and elevated motivation to search (Saar *et al.*, 2017; Bega *et al.*, 2020; Gilad *et al.*, 2022a). The congeneric species *C. cursor* was also studied in the laboratory and was shown to associate landmarks with the correct routes to the food reward (Chameron *et al.*, 1998; Schatz *et al.*, 1999). *Cataglyphis* ants are diurnal individual foragers with no recruitment other than stimulating additional workers to leave the nest if food is found (Lenoir *et al.*, 2009; Amor *et al.*, 2010). This lack of recruitment leads to individual learning by each worker. If recruitment did take place, it would be sufficient for a single worker to learn the way to the food and then recruit the others. A system of individual foragers, however, is less affected by a single event of one worker discovering food, and the colony's learning performance here is the true sum of the behavior of all the individual foragers (rather than a single worker recruiting all the others). *Cataglyphis* spp. forage over long distances in arid habitats, are known for their navigational abilities, and have served as models for studies on central forager navigation (Cheng & Wehner, 2002; Wehner, 2003; Mangan & Webb, 2012).

We examined whether prior experience in a complex maze would improve the food detection ability, food exploitation, and hence foraging of a group of workers competing against another similar sized group that had only been trained in a simple maze. We hypothesized that experience would provide the complex maze trained group with an advantage over the simple maze trained group when both competed in a complex maze. We expected experience to be more important in larger groups than in smaller ones, because in larger groups more workers leave the colony to forage and acquire experience. If spatial experience is indeed of major importance, we expected smaller but trained worker groups to arrive faster and with more workers at the food source than larger untrained worker groups. If it is not, then larger groups should arrive first at the food owing to the positive correlation between group size and the number of foragers.

Materials and methods

The experiments were conducted in 2018–2020. *C. niger* colonies were collected from the Tel Baruch sand dunes (32.1283N, 34.7867E). This area comprises mostly

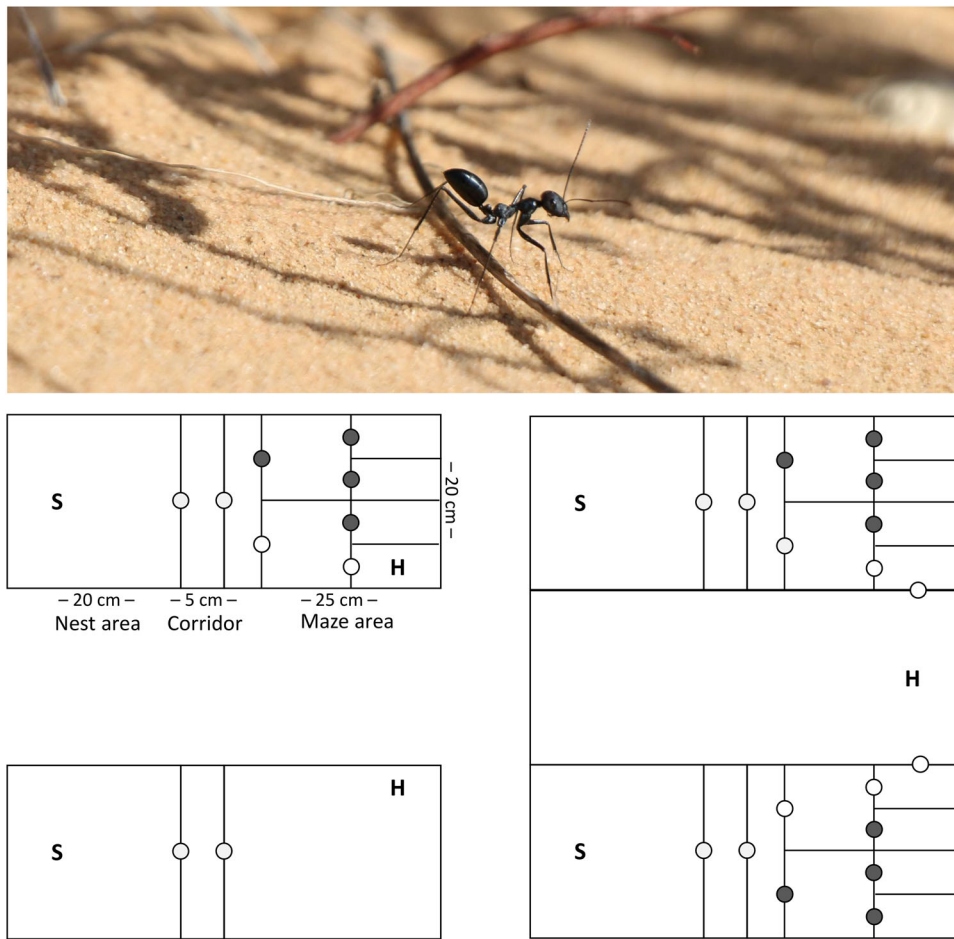


Fig. 1 Top: A *Cataglyphis niger* forager in Tel Baruch sand dunes (photographed by Arik Dorfman). Left: A scheme of the two mazes used in the training phase (the complex and the simple one, above and below, respectively). S and H stand for the start point or the nest area, and the honey or the food reward, respectively. White and gray circles stand for a door leading to the food reward and a dead-end, respectively. Right: The mazes in the competition phase were attached to a shared arena, in which the food reward was provided.

stabilized and semistabilized sand dunes and quite dense vegetation (Saar *et al.*, 2018). Foraging ants consequently frequently encounter obstacles, requiring the use of less direct routes to the food sources (Bega *et al.*, 2019). All the experimental ant colonies were transferred to laboratory, and each colony was maintained at $\sim 28^{\circ}\text{C}$, 12 : 12 L : D, in a plastic, 4-L box, filled with sand and water tubes without food for a week, which is sufficient to motivate the workers to forage (similar to Gilad *et al.*, 2022a).

Experiment 1: Worker groups of equal sizes competing in a complex maze

We collected 80 *C. niger* colonies (184.2 ± 95.7 [60, 504]; mean colony size ± 1 SD [range]). About half a day

before the experiment, we separated groups of 8, 17, 34, or 55 individuals from the colony and moved each group to a white Plexiglas nest (20×20 cm; Fig. 1), containing water tubes. Although these groups are smaller than colonies in nature, previous studies have demonstrated that such groups will forage and collect food in the laboratory (Gilad *et al.*, 2020b, 2022a). Whereas such small groups may not directly display aggression, they might still compete and prevent competitors from accessing resources or deplete them. The workers were chosen randomly from all colony workers, while seeking to allocate workers of similar body sizes to each treatment. The nest was attached to a corridor (5×20 cm), leading to an open arena (25×20 cm), where a maze was inserted. The experiment comprised two phases: training and competition. Each colony was used only once in each experiment.

Pairs of competing worker groups always originated from different colonies.

Training phase: Pairs of worker groups of equal sizes were assigned separately to either training in a complex maze inside the open arena, as described above, or training in a simple maze (Fig. 1). Both mazes were 25×20 cm ($l \times w$) built with opaque Plexiglas. The simple maze comprised a single cell. In the complex maze, the first cell was a narrow rectangle leading to two cells, each of them leading to two additional cells (Fig. 1). The cells were connected via an opening of 1 cm diameter, closed by a small door. The workers could easily move on the maze surface and through the openings. The training procedure was similar to that in Saar *et al.* (2017). We let the worker groups explore the maze and search for a 6-cm Petri dish containing 0.5 g of 50% diluted honey. We documented the food-discovery time (i.e., the time taken for the first worker to reach the food reward from the beginning of each run). The experiment ended 10 min following the food discovery by the first worker and all workers were returned to the nest and the maze was sealed. Thus, the experiment duration varied, depending on the latency to food discovery. If the food was not discovered, the experiment was stopped after 50 min, which was then considered as the food-discovery time. We repeated this procedure three times for each worker group under the same conditions. Three runs in the same maze are sufficient to shorten the maze-solving time and workers kept leaving the nest to forage in all runs (Saar *et al.*, 2017, 2020; Bega *et al.*, 2020). There was a 30-min break between successive runs, and the mazes were wiped with alcohol between each run. The experiment incorporated 80 colonies, 20 in each of the four size groups, resulting in a sample size of 10 pairs per group size.

Competition phase: Half an hour following the training phase, we opened up the mazes of the two competing worker groups, located next to the initial location of the food reward, to an additional arena, located in-between the mazes (55×20 cm), and containing a single food reward in the center over which both workers groups could compete (Fig. 1). Both worker groups, that previously trained in a complex maze and that trained in a simple maze, were tested in the complex maze (identical to that used in the training phase of one of the groups), to study the effect of prior training in the complex maze on competition. The distance between the two nests and the food reward was identical. We measured the time required for the first worker to discover the food reward (food-discovery time), and the number of workers that arrived at the food reward until 10 min post initial food-discovery time (workers feeding; similar to Saar *et al.*, 2017; Bega *et al.*, 2020). The latter was determined based on videos

of the experiment. The two variables are correlated (faster initial discovery time resulted in more workers arriving at the food). Furthermore, the number of workers feeding is correlated with the amount of food collected (Saar *et al.*, 2017 and unpublished data), and therefore represents foraging success. Competition is revealed here in two main forms: first, workers may restrict the access of competitors to the food reward or interact aggressively with them (interference); and second, the resources can be depleted by one group of workers (exploitation). We therefore documented whether antagonistic interactions occurred among workers, expressed either in fights between pairs of workers from competing groups or the invasion of workers into the area of the opponent maze or nest. All tests during this phase were filmed.

Experiment 2: Small groups of trained workers competing against larger untrained ones

Here we focused on groups numbering 34 workers following the results of Experiment 1, which had shown that the contribution of training to competition success was the greatest in a group of this size (see Results). We examined the competition outcome of groups of 34 workers trained to solve the complex maze, against untrained (i.e., only trained to solve a simple maze) larger groups of either 45 or 55 workers. For this purpose, we collected an additional 40 colonies (240.9 ± 139.0 [55, 617]; mean colony size ± 1 SD [range]), 20 for each group size (34 vs. 45 and 34 vs. 55 workers). All collected colonies underwent the same procedure of either complex or simple maze training followed by the competition phase, as in Experiment 1. We compared the findings from this uneven competition (34 vs. 45 or 55 workers) with the even competition (34 workers in both groups) of Experiment 1. Each of the three group sizes (one even and two uneven) contributed 10 replications. If the contribution of spatial experience is major, we expected the trained smaller worker groups to arrive at the food faster and in greater numbers than the untrained larger worker groups, whereas if the contribution of spatial experience is minor, larger groups should discover the food faster, independent of training.

Data analyses

We subtracted the food-discovery time of the untrained worker group from that of the trained one (Δ food-discovery time). The positive and negative values indicated that the untrained worker group had discovered the food either faster or slower, respectively, than the trained

one. We also subtracted the number of feeding workers belonging to the untrained group from that of the trained group (Δ workers feeding). Positive values indicated that more workers of the trained group than of the untrained group had fed on the food reward.

Next, we sought to determine whether the trained worker groups discovered the food reward faster or exploited it better by having more workers feeding. Because data were not normally distributed, we used a bootstrap procedure with 10 000 replications (using MATLAB R2021b), which does not assume a normal distribution (Dixon, 2001), to calculate the coefficient intervals (hereafter, CIs) for Δ food-discovery time and Δ workers feeding. If zero is not included in the 95% CIs, this indicates that one of the groups has an advantage. Regarding food-discovery time, all 40 pairs in the first experiment and all 30 pairs in the second experiment were included in the analysis. Regarding the number of workers arriving at the food, and based on the films, we could identify worker source (colony identity) in 32/40 and 25/30 worker groups in the first and second experiment, respectively. As we conducted 12 bootstrap tests, we used the Holm-Bonferroni correction, set α to $0.05/(12 - \text{rank number} + 1)$, to correct for multiple testing, and referred only to P values lower than this threshold as significant (rank number equals the test rank sorted according to significance level).

Further analyses of two additional time-related variables, food discovery as a binary variable (whether the trained group arrived faster or not), and agonistic interactions are available in the Supplementary Material.

Results

Experiment 1: Worker groups of equal sizes competing in a complex maze

The trained worker groups discovered the food faster only in the 34 worker group (estimated $P = 0.0004$ or 4 of 10 000 bootstrap replications, threshold set to 0.0045; Cohen's $d = 1.663$; Fig. 2A, B). Training had no effect in all other group sizes (CIs overlap zero; Fig. 2A, B). The number of workers feeding was higher in the trained groups of 34 workers ($P = 0.0002$, threshold set to 0.0042; Cohen's $d = 1.509$; Fig. 2C, D). Although the untrained groups of 55 workers appeared to arrive in higher numbers at the food reward ($P = 0.0067$, threshold set to 0.0050), the P value was higher than the threshold we set, and we therefore consider this result as not significant. In 25 of the 40 competition events, workers of one group invaded the maze/nest area of the other group, lead-

ing in some cases to antagonistic interactions (biting or dragging). Of the observed 40 aggressive events, 22 were carried over by the trained groups and 18 by the untrained ones.

Experiment 2: Small groups of trained workers competing against larger untrained ones

Although the groups of 34 trained workers discovered the food faster than untrained groups of 34 workers (see the results of Experiment 1), the advantage of training (i.e., faster food discovery and more workers reaching the food) disappeared when the untrained opponent group size was larger. The CIs of both Δ food-discovery time and Δ workers feeding overlapped zero, indicating no advantage to any of the competing groups (Fig. 3). In 18 of the 20 additional competition events carried out in Experiment 2 (34 vs. 45 and 34 vs. 55 workers), workers of one group invaded the maze/nest of the other group, leading in some cases to antagonistic interactions (biting or dragging). In total, we counted 32 aggressive events, of which 13 were performed by the trained worker groups.

Discussion

We examined here in the ant *Cataglyphis niger* whether familiarity with a complex maze enhances foraging success when searching in the same complex maze and competing against a group of workers untrained in the same maze. We found that foraging experience in a complex maze could lead to faster food discovery under competition conditions and to more workers feeding. This advantage however was limited only to the intermediate group size tested, was absent in smaller or larger groups, and was mitigated by a larger group size of untrained opponents. Our hypothesis that experience contributes to food discovery and exploitation under conditions of direct competition is therefore only partially supported.

Why the advantage of training was only evident in the intermediate group size of 34 workers is intriguing. Training smaller groups might prevent enough workers from gaining sufficient experience in foraging. In the studied species, as well as in several other ant species, because only $\sim 10\%$ of the workers contribute to foraging (Porter & Jorgensen, 1981; Retana & Cerdá, 1990; Bega *et al.*, 2019), it is probable that not enough workers in the small groups acquired sufficient exposure to the maze. On the other hand, colonies over a certain size may rely less on experience and instead “flood” the maze with foragers, which may ultimately eliminate the advantage of training. Our results suggest that experience may be

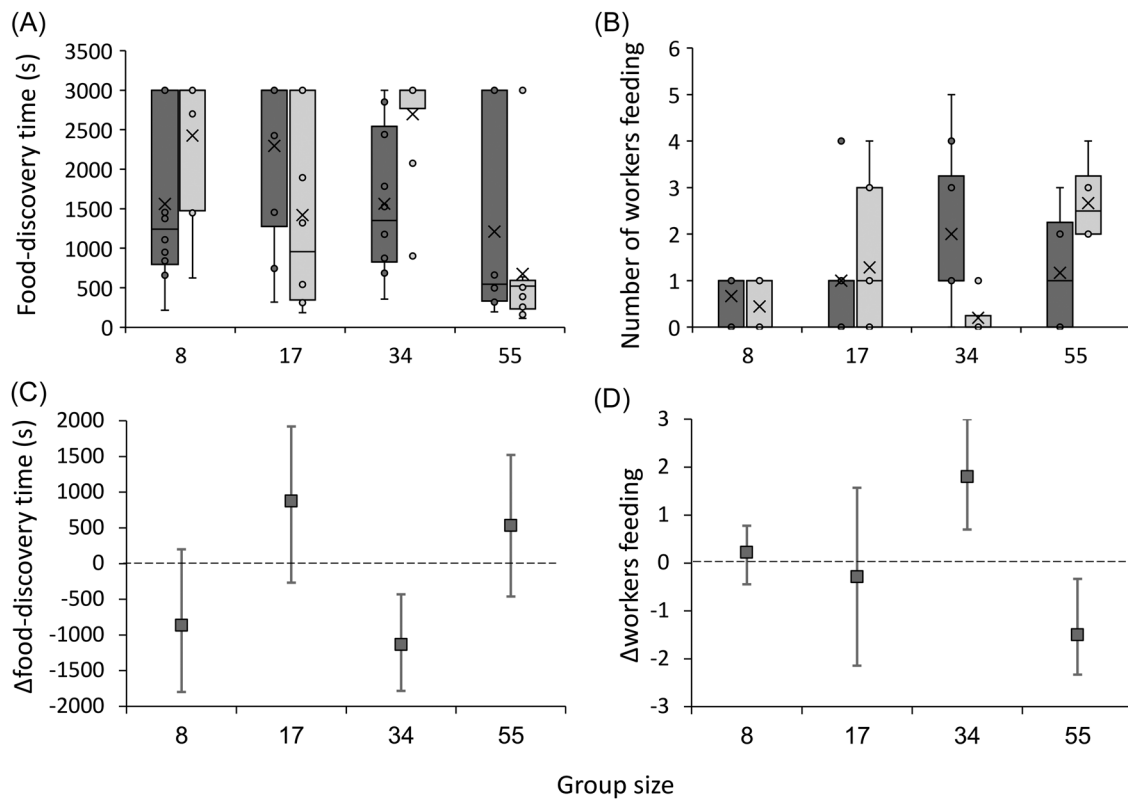


Fig. 2 (A) Food-discovery time, (B) the number of workers feeding on the food reward, (C) Δ food-discovery time (the untrained worker group subtracted from the trained one), and (D) Δ workers feeding (the untrained worker group subtracted from the trained one) in the experiment with groups of workers of equal sizes. (A, B) Trained worker groups appear in dark gray and untrained ones in bright gray. Medians (horizontal lines), quartiles, outliers (dots), and the entire range are presented. (C, D) Means \pm 95% confidence intervals are presented.

important for young, small colonies during their growth period, with the effect of training, although size-specific, relevant for all colonies during early ontogeny, as all start with a single queen and small colony size. It is probable that the contribution of each individual worker to small colonies is higher than that in larger colonies, and it is therefore more profitable for workers in small colonies to forage more efficiently. Interference appears to have been the main competition type in our experiment, as evident in the frequent antagonistic interactions between workers from different groups (e.g., invading the nest of the other group). That said, our aim was not to quantify the relative weight of interference and exploitation, but, rather, to uncover a mechanism by which experience might contribute to foraging success under competition conditions.

We suggest that learning took place during the training phase, albeit which of the two—spatial learning or associative learning—was dominant here is uncertain. Trained workers could either learn the faster way to reach the food reward (spatial learning) or could associate the

opening of the nest door with the existence of food nearby (associative learning). There is evidence for both from similar experiments with the same species and in the current set-up (Bega *et al.*, 2020; Gilad *et al.*, 2022a). Independent of the exact learning mechanism, we suggest that our experiment provides some support for a possible contribution of learning under direct competition conditions. Specifically, trained groups of 34 workers discovered the food faster under competition conditions than untrained groups. Becoming familiar with the habitat is necessary when conditions change or following nest relocation. We have no data on nest relocation in the studied species, but the congeneric *Cataglyphis iberica* occasionally relocates its nest following aggression with another ant species (Cerdá & Retana, 1998). Losing habitat familiarity could be an additional cost of relocation on top of moving and digging a new nest, especially when there are many other nests in the vicinity.

Very few experiments have examined the contribution of learning under competition conditions. One exception

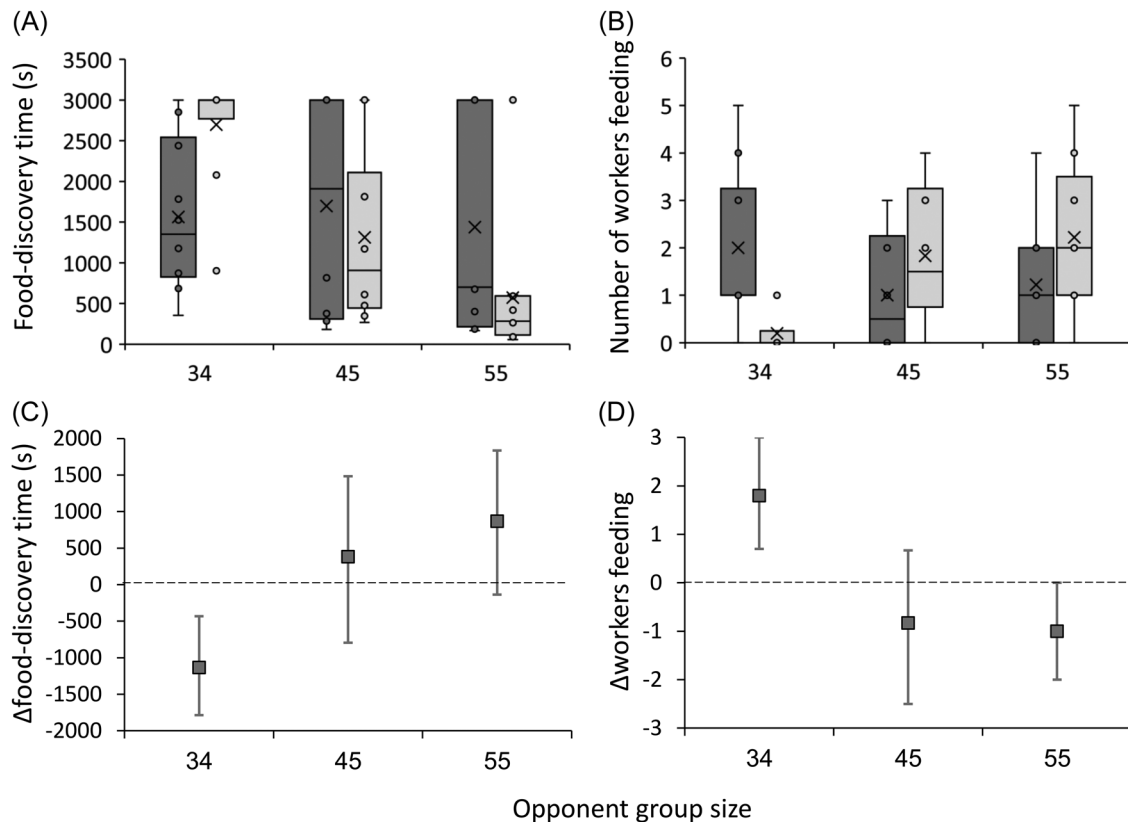


Fig. 3 (A) Food-discovery time, (B) the number of workers feeding on the food reward, (C) Δ food-discovery time (the untrained worker group subtracted from the trained one), and (D) Δ workers feeding in the experiment with worker groups of unequal sizes. Groups trained in the complex maze comprised 34 workers while their opponents differed in number (34, 45, or 55 workers). (A, B) Trained worker groups appear in dark gray and untrained ones in bright gray. Medians (horizontal lines), quartiles, outliers (dots), and the entire range are presented. (C, D) Means \pm 95% confidence intervals are presented.

is that by Mery & Kawecki (2003), who selected for improved learning ability in flies and demonstrated that those flies were nonetheless inferior when competing against a line that had not undergone artificial selection for improved learning (reviewed in Kawecki, 2010). However, in their experiment, the two lines did not compete against one another but against a reference line. Although testing competition against a reference line is common in the literature (e.g., Santos *et al.*, 1992), the two competitors may each interact differently with a reference line and direct competition, as performed here, constitutes a stronger experimental design.

A common coexistence mechanism of competing species is that of the dominance-discovery trade-off, with some species detecting resources faster and other species either dominating resources or exploiting them more efficiently (Adler *et al.*, 2007; LeBrun & Feener, 2007; Perfecto & Vandermeer, 2011). Our studied species, *C. niger*, which forages individually, is probably inferior in

direct competition against other ant species that can recruit many workers. A high ability for spatial learning, experience, or habitat familiarity, may compensate for *C. niger*'s competitive inferiority and allow its coexistence with worker-recruiting species, especially considering that *C. niger* forages for ephemeral resources. A similar mechanism of relying more on spatial learning than on group size may assist smaller colonies to coexist with larger ones of the same species, which can elevate their foraging performance simply by increasing the number of foraging workers. Furthermore, colonies usually dominate the area around the nest entrance. Spatial learning may contribute to expanding this area of domination, even for small colonies, and thus provide such colonies with a competitive advantage. All these are suggestions that remain to be tested.

It is important to note that competing animals have often been assumed to perform similarly over time independent of experience (Kotler & Mitchell, 1995). The

present findings suggest that, at least under some conditions (here, groups of 34 trained workers), experience may change the outcome of competition and should be considered if the experiment results differ from the theoretical predictions. Due to our low sample size per group (10 pairs of colonies), we believe that our results underestimate the contribution of training to foraging success. Future studies should increase the sample size and examine additional conditions under which training may contribute to competition success. Increasing the sample size can compensate for cases in which no workers left the nest to forage, perhaps because no foragers were selected when composing the competing groups. This is clearly more relevant for small groups. Future experiments should also match colonies with both familiar neighbors and more distant colonies. The type of response to neighbors may be either stronger or weaker, if such neighboring colonies represent a lower or higher threat, respectively, than that of other colonies. These two alternative hypotheses are termed the “dear enemy effect” and “nasty neighbor effect” (cf. Heinze *et al.*, 1996; Newey *et al.*, 2010). The interaction of spatial learning with the distance between competing colonies has never been previously studied. Furthermore, examining the same question in the field with competing colonies is an important future step to understand whether the results obtained in the laboratory hold also true at a larger scale in the ant’s natural habitat.

In conclusion, we have demonstrated here the moderate contribution of spatial experience to food discovery in ants under competition conditions and under a limited number of scenarios. We suggest that learning or experience should be considered as a possible mechanism enabling coexistence between competing individuals or species.

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Author contributions

A.S. conceived and designed the study and significantly contributed to the statistical analysis and writing. B.A., D.B. A.D., M.K., M.H.R., and T.G. collected the colonies, did the experiment, and analyzed the videos. I.S. did the statistics and wrote the manuscript. S.F. contributed significantly to the writing process. All authors read the manuscript and contributed to the writing procedure.

Disclosure

We declare no conflict of interest.

References

- Abrams, P. (1975) Limiting similarity and the form of competition coefficient. *Theoretical Population Biology*, 8, 356–375.
- Adler, F.R., LeBrun, E.G. & Feener, D.H. (2007) Maintaining diversity in an ant community: modeling, extending, and testing the dominance-discovery trade-off. *American Naturalist*, 169, 323–333.
- Adler, P.B., Smull, D., Beard, K.H., Choi, R.T., Furniss, T., Kulmatiski, A. *et al.* (2018) Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters*, 21, 1319–1329.
- Amor, F., Ortega, P., Cerdá, X. & Boulay, R. (2010) Cooperative prey-retrieving in the ant *Cataglyphis floricola*: an unusual short-distance recruitment. *Insectes Sociaux*, 57, 91–94.
- Bega, D., Samocha, Y., Yitzhak, N., Saar, M., Subach, A. & Scharf, I. (2019) The effect of maze complexity on maze-solving time in a desert ant. *Behavioural Processes*, 166, 103893.
- Bega, D., Samocha, Y., Yitzhak, N., Saar, M., Subach, A. & Scharf, I. (2020) Non-spatial information on the presence of food elevates search intensity in ant workers, leading to faster maze solving in a process parallel to spatial learning. *PLoS ONE*, 15, e0229709.
- Bolin, A., Smith, H.G., Lonsdorf, E.V. & Olsson, O. (2018) Scale-dependent foraging tradeoff allows competitive coexistence. *Oikos*, 127, 1575–1585.
- Bolnick, D.I. (2001) Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. *Nature*, 410, 463–466.
- Bolnick, D.I. (2004) Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution; International Journal of Organic Evolution*, 58, 608–618.
- Cerdá, X., Arnan, X. & Retana, J. (2013) Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology. *Myrmecological News*, 18, 131–147.
- Cerdá, X. & Retana, J. (1998) Interference interactions and nest usurpation between two subordinate ant species. *Oecologia*, 113, 577–583.
- Chameron, S., Schatz, B., Pastergue-Ruiz, I., Beugnon, G. & Collett, T.S. (1998) The learning of a sequence of visual patterns by the ant *Cataglyphis cursor*. *Proceedings of the Royal Society of London B*, 265, 2309–2313.
- Charter, M., Leshem, Y. & Izhaki, I. (2013) Asymmetric seasonal nest site competition between Great Tits and House Sparrows. *Journal of Ornithology*, 154, 173–181.

- Cheng, K. & Wehner, R. (2002) Navigating desert ants (*Cataglyphis fortis*) learn to alter their search patterns on their homebound journey. *Physiological Entomology*, 27, 285–290.
- Dixon, P.M. (2001) The Bootstrap and the Jackknife: describing the precision of ecological indices. *Design and Analysis of Ecological Experiments* (eds. S.M. Scheiner & J. Gurevitch), pp. 267–288. Oxford University Press, Oxford.
- Dukas, R. & Real, L.A. (1993) Effects of recent experience on foraging decisions by bumble bees. *Oecologia*, 94, 244–246.
- Dyer, F.C. (1998) Spatial cognition: lessons from central-place foraging insects. *Animal Cognition in Nature* (eds. R.P. Balda, I.M. Peppeberg & A.C. Kamil), pp. 119–154. Academic Press, San Diego, CA, USA.
- Erős, K., Maák, I., Markó, B., Babik, H., Ślipiński, P., Nicoară, R. *et al.* (2020) Competitive pressure by territorials promotes the utilization of unusual food source by subordinate ants in temperate European woodlands. *Ethology Ecology & Evolution*, 32, 457–465.
- Fellers, J.H. (1987) Interference and exploitation in a guild of woodland ants. *Ecology*, 68, 1466–1478.
- Gilad, T., Dorfman, A., Subach, A. & Scharf, I. (2022b) Leg or antenna injury in *Cataglyphis* ants impairs survival but does not hinder searching for food. *Current Zoology*, <https://doi.org/10.1093/cz/zoab027>.
- Gilad, T., Dorfman, A., Subach, A., Libbrecht, R., Foitzik, S. & Scharf, I. (2022a) Evidence for the effect of brief exposure to food, but not learning interference, on maze solving in desert ants. *Integrative Zoology*, Online ahead of print. <https://doi.org/10.1111/1749-4877.12622>.
- Grant, P.R. & Grant, B.R. (2006) Evolution of character displacement in Darwin's finches. *Science*, 313, 224–226.
- Gurevitch, J., Morrow, L.L., Wallace, A. & Walsh, J.S. (1992) A meta-analysis of competition in field experiments. *American Naturalist*, 140, 539–572.
- Heinze, J., Foitzik, S., Hippert, A. & Hölldobler, B. (1996) Apparent dear-enemy phenomenon and environment-based recognition cues in the ant *Leptothorax nylanderi*. *Ethology*, 102, 510–522.
- Hills, T.T., Todd, P.M., Lazer, D., Redish, A.D., Couzin, I.D. & Group C.S.R. (2015) Exploration versus exploitation in space, mind, and society. *Trends in Cognitive Sciences*, 19, 46–54.
- Johnson, R.A. (1991) Learning, memory, and foraging efficiency in two species of desert seed-harvester ants. *Ecology*, 72, 1408–1419.
- Kawecki, T.J. (2010) Evolutionary ecology of learning: insights from fruit flies. *Population Ecology*, 52, 15–25.
- Katz, K. & Naug, D. (2015) Energetic state regulates the exploration-exploitation trade-off in honeybees. *Behavioral Ecology*, 26, 1045–1050.
- Keddy, P.A. (2001) *Competition* (2nd edn.). Kluwer, Dordrecht.
- Kembro, J.M., Lihoreau, M., Garriga, J., Raposo, E.P. & Bartumeus, F. (2019) Bumblebees learn foraging routes through exploitation-exploration cycles. *Journal of the Royal Society Interface*, 16, 20190103.
- Kotler, B.P. & Mitchell, W.A. (1995) The effect of costly information in diet choice. *Evolutionary Ecology*, 9, 18–29.
- LeBrun, E.G. & Feener, D.H. (2007) When trade-offs interact: balance of terror enforces dominance discovery trade-off in a local ant assemblage. *Journal of Animal Ecology*, 76, 58–64.
- Lenoir, A., Aron, S., Cerdá, X. & Hefetz, A. (2009) *Cataglyphis* desert ants: a good model for evolutionary biology in Darwin's anniversary year—a review. *Israel Journal of Entomology*, 39, 1–32.
- Mangan, M. & Webb, B. (2012) Spontaneous formation of multiple routes in individual desert ants (*Cataglyphis velox*). *Behavioral Ecology*, 23, 944–954.
- McGlynn, T.P. (2000) Do Lanchester's laws of combat describe competition in ants? *Behavioral Ecology*, 11, 686–690.
- Mery, F. & Kawecki, T.J. (2003) A fitness cost of learning ability in *Drosophila melanogaster*. *Proceedings of the Royal Society of London B*, 270, 2465–2469.
- Meszéna, G., Gyllenberg, M., Pásztor, L. & Metz, J.A.J. (2006) Competitive exclusion and limiting similarity: a unified theory. *Theoretical Population Biology*, 69, 68–87.
- Mitchell, W.A., Abramsky, Z., Kotler, B.P., Pinshow, B. & Brown, J.S. (1990) The effect of competition on foraging activity in desert rodents: theory and experiments. *Ecology*, 71, 844–854.
- Monk, C.T., Barbier, M., Romanczuk, P., Watson, J.R., Alós, J., Nakayama, S. *et al.* (2018) How ecology shapes exploitation: a framework to predict the behavioural response of human and animal foragers along exploration-exploitation trade-offs. *Ecology Letters*, 21, 779–793.
- Newey, P.S., Robson, S.K. & Crozier, R.H. (2010) Weaver ants *Oecophylla smaragdina* encounter nasty neighbors rather than dear enemies. *Ecology*, 91, 2366–2372.
- Orians, G.H. & Pearson, N.E. (1979) On the theory of central place foraging. *Analysis of Ecological Systems* (eds. D.J. Horn, R.D. Mitchell, & G.R. Stairs), pp. 155–177. Ohio State University Press, Columbus, Ohio, USA.
- Palmer, T.M. (2004) Wars of attrition: colony size determines competitive outcomes in a guild of African acacia ants. *Animal Behaviour*, 68, 993–1004.
- Parr, C.L. & Gibb, H. (2010) Competition and the role of dominant ants. *Ant Ecology* (eds. L. Lach, C.L. Parr & K.L. Abbott), pp. 77–96. Oxford University Press, Oxford, UK.
- Perfecto, I. & Vandermeer, J. (2011) Discovery dominance tradeoff: the case of *Pheidole subarmata* and *Solenopsis geminata* (Hymenoptera: Formicidae) in neotropical pastures. *Environmental Entomology*, 40, 999–1006.

- Perrin, M.R. & Kotler, B.P. (2005) A test of five mechanisms of species coexistence between rodents in a southern African savanna. *African Zoology*, 40, 55–61.
- Porter, S.D. & Jorgensen, C.D. (1981) Foragers of the harvester ant, *Pogonomyrmex owyheei*: a disposable caste. *Behavioral Ecology and Sociobiology*, 9, 247–256.
- Retana, J. & Cerdá, X. (1990) Social organization of *Cataglyphis cursor* ant colonies (Hymenoptera, Formicidae): inter-, and intraspecific comparisons. *Ethology*, 84, 105–122.
- Robinson, E.J., Feinerman, O. & Franks, N.R. (2012) Experience, corpulence and decision making in ant foraging. *Journal of Experimental Biology*, 215, 2653–2659.
- Saar, M., Gilad, T., Kilon-Kallner, T., Rosenfeld, A., Subach, A. & Scharf, I. (2017) The interplay between maze complexity, colony size, learning and memory in ants while solving a maze: a test at the colony level. *PLoS ONE*, 12, e0183753.
- Saar, M., HersHKovitz, D., Amano, O., Bega, D., Subach, A. & Scharf, I. (2020) The effect of food preference, landmarks, and maze shift on maze-solving time in desert ants. *Behaviour*, 157, 629–665.
- Saar, M., Subach, A., Reato, I., Liber, T., Pruitt, J.N. & Scharf, I. (2018) Consistent differences in foraging behavior in 2 sympatric harvester ant species may facilitate coexistence. *Current Zoology*, 64, 653–661.
- Santos, M., Fowler, K. & Partridge, L. (1992) On the use of tester stocks to predict the competitive ability of genotypes. *Heredity*, 69, 489–495.
- Schatz, B., Chameron, S., Beugnon, G. & Collett, T.S. (1999) The use of path integration to guide route learning in ants. *Nature*, 399, 769–772.
- Schmitt, R.J. (1996) Exploitation competition in mobile grazers: trade-offs in use of a limited resource. *Ecology*, 77, 408–425.
- Steinwascher, K. (1978) Interference and exploitation competition among tadpoles of *Rana utricularia*. *Ecology*, 59, 1039–1046.
- Svanbäck, R. & Bolnick, D.I. (2007) Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B*, 274, 839–844.
- Tanner, C.J. (2006) Numerical assessment affects aggression and competitive ability: a team-fighting strategy for the ant *Formica xerophila*. *Proceedings of the Royal Society B*, 273, 2737–2742.
- Tiong, G.J. & Morse, D.H. (2021) Discovery-exploitation trade-offs in a multispecies ant-treehopper mutualism: foraging strategy differences and temporal changes across ant attendance behaviors. *Journal of Insect Behavior*, 34, 173–185.
- VanderSal, N.D. (2008) Rapid spatial learning in a velvet ant (*Dasymutilla coccineohirta*). *Animal Cognition*, 11, 563–567.
- Wehner, R. (2003) Desert ant navigation: how miniature brains solve complex tasks. *Journal of Comparative Physiology A*, 189, 579–588.
- Wolf, H. (2008) Desert ants adjust their approach to a foraging site according to experience. *Behavioral Ecology and Sociobiology*, 62, 415–425.
- Ydenberg, R.C., Giraldeau, L.A. & Kramer, D.L. (1986) Interference competition, payoff asymmetries, and the social relationships of central place foragers. *Theoretical Population Biology*, 30, 26–44.
- Zirkle, D.F., Dawson, P.S. & Lavie, B. (1988) An experimental analysis of the genetic relationships among life-history traits and emigration behavior in *Tribolium castaneum*. *Oikos*, 53, 391–397.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supplementary Material Additional time-related variables, food discovery as a binary variable, and agonistic interactions are further analyzed in the Supplementary Material. The dataset is available there too.