



# Habitat complexity and predictability effects on finding and collecting food when ants search as cooperative groups

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Cooperatively foraging groups have two sequential goals: to find food and thereafter efficiently exploit or retrieve it. Previous research has largely focused on searching behaviours of individuals or organization of food retrieval processes, rather than on how groups initially distribute themselves to find ephemeral food items that are unpredictable in time and space. In the present study, we examined how Argentine ants, *Linepithema humile*, search environments in anticipation of food appearing briefly in areas with differing spatial complexity. Nests were connected to three foraging arenas containing 1, 9 or 25 cells. Food appeared briefly in one cell each day, either randomly or more predictably in distant cells (but equally often in each arena). We recorded the number of ants in cells when food had not been recently present, and thereafter whether ants successfully located the food when presented. Surprisingly, as food location became more predictable, ants found it less frequently. Foragers were located more often in cells closer to the nest (i.e. at information 'choke points' that returning foragers needed to traverse), and in cells with higher connectivity and greater centralness within foraging arenas. Such distributions reduce search coverage area but likely increase information transmission. Thus, it appears that *L. humile* foragers distribute themselves to favour rapid recruitment when food is found rather than maximizing food encounter rates. Although the reduced foraging success with more predictably located food suggests that ants did not adjust expectations in a Bayesian manner within arenas towards individual cells, they did appear Bayesian across arenas. Because foragers missed food more often in higher-complexity arenas than in lower-complexity arenas, this could increase perceptions that the latter are more rewarding. Shifts in distributions were consistent with such biased perceptions. Future studies to determine whether other group-foraging species use analogous solutions would be highly useful.

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Foragers often face a changing landscape in terms of resource location and availability. Food can be distributed heterogeneously across the habitat (Lima, 1984), and individual patches can be highly ephemeral and subject to dissipation or exploitation and depletion by competitors (Naug & Arathi, 2007). Given that a forager's first goal is to effectively encounter potential food items, it is expected that how animals search their environment will change depending on the abundance or type of food present, current hunger state, likelihood of encountering dangerous competitors and variability of patch quality over time and space. There are a number of such examples of behaviour tracking changing conditions. Thrushes alter the spatial distribution of their sampling depending on food density (Smith, 1974). Ants vary their sampling

patterns, both spatially and temporally, depending on whether carbohydrates or protein are available (Traniello, Kozol, & Fournier, 1992). Houseflies increase their turning rate and reduce their speed after recently eating (Hassell & Southwood, 1978). In *Formica* ants, smaller foragers will avoid sites at which they risk being attacked and larger ones may spend more time at these sites in a defensive mode (Kay & Rissing, 2005; Tanner, 2008). Griffon vultures, *Gyps fulvus*, routinely forage in variable and unpredictable environments, but when given a choice, prefer more predictable environments (Monsarrat et al., 2013).

Intrinsic to adopting an effective search strategy, therefore, is learning about one's environment through balancing between past and present experiences (Stephens & Krebs, 1986). Combining older with newer information to alter expectations is known as Bayesian updating (Valone, 2006). Behaviour consistent with a Bayesian sampling and learning regime has been observed in a wide variety of taxonomic groups, including birds (Alonso, Alonso, Bautista, & Muñoz-Pulido, 1995; Lima, 1984, 1985; Olsson, Wiklander,

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Holmgren, & Nilsson, 1999; Valone, 1991, 1992; van Gils, Schenk, Bos, Piersma, & Moore, 2003), mammals (Spencer, 2012; Valone & Brown, 1989) and social insects (Naug & Arathi, 2007; Nonacs & Soriano, 1998). The value of an updating scheme can depend on the environment. For example, black-chinned hummingbirds, *Archilochus alexandri*, do not gain from being Bayesian in highly variable environments and generally do not update. In low-variance environments, however, most birds appear to update, and Bayesian-like foragers are the most efficient (Valone, 1992).

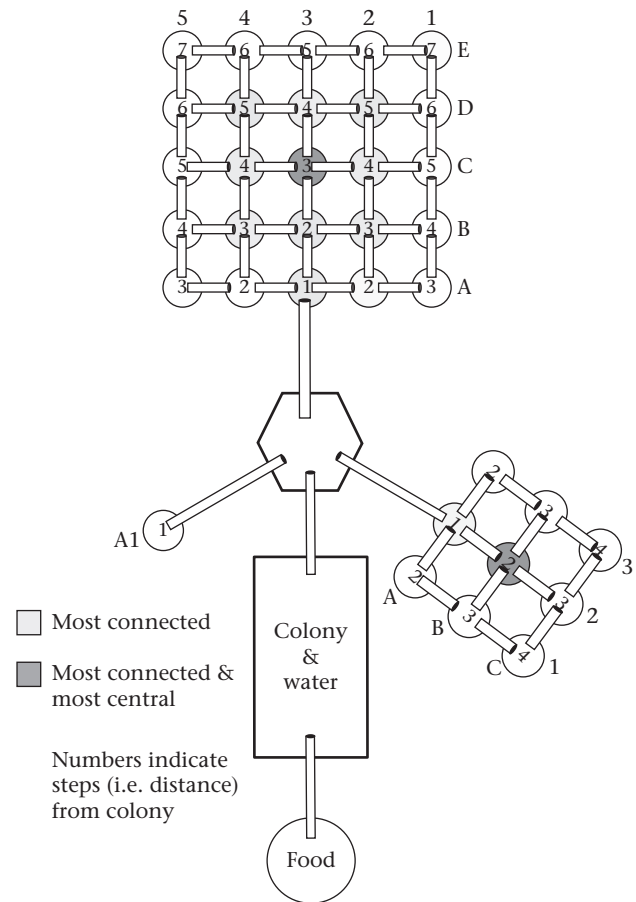
Group-foraging animals such as ants add a second dimension to the search algorithm. Search entails not only how individual foragers move but also group processes, such as how individuals interact and distribute themselves. These dynamics are evident in some species of desert ants that forage individually when food is abundant but forage together in narrow columns and circular areas when food is scarce (Bernstein, 1975). In addition to how best to initially find food, social insect colonies often face another distinct organizational problem—how best to retrieve food to the nest. If successful foragers do not recruit others to the found location (e.g. *Polistes* paper wasps; Reeve, 1991), then optimal foraging models such as central place foraging are useful in predicting how individuals gather food (Azevedo, Medeiros, & Araújo, 2014), or where nests are located relative to food patches (Holway & Case, 2000).

In more behaviourally complex cooperatively foraging species, food discovery by an individual can lead to recruitment of many others to the discovery site. This presents an interesting discovery–dominance trade-off (Davidson, 1998). Dispersing a foraging contingent widely will cover more area and therefore increase discovery rates. However, this simultaneously makes it difficult to quickly recruit many foragers from nonproductive sites to dominate and control the rewarding area. An alternative strategy would be to clump potential recruits at key locations where they can be quickly encountered and summoned (Roulston & Silverman, 2002); such a strategy has been observed in *Lasius niger* ants (Depickère, Fresneau, & Deneubourg, 2004b). This tactically reduces the total amount of area that all the foragers can search, but if found food is indeed ephemeral in nature, or competitors can potentially purloin it, then being able to quickly acquire it may offset reduced encounter rates.

We focus on examining this one stage of the group-foraging process: how colonies of the cooperatively foraging Argentine ant, *Linepithema humile*, search their habitat in anticipation of finding a shifting and ephemeral food source. We experimentally varied the spatial complexity of the search areas and the predictability of the exact location where food appeared. We were particularly interested in determining whether the spatial distribution of foragers influences how rapidly they might be recruited and the degree to which spatial patterns adjust in a Bayesian-like manner relative to information available from the environment.

## METHODS

We set up three replicate nests of Argentine ants (*L. humile*) containing approximately 10–15 queens and 300–500 worker ants collected from a large population in Westwood, California, U.S.A. The ants nested in an open plastic container in a covered depression of a floor made of plaster of Paris, which was kept moist for nest humidity (Fig. 1). The sides of each container were coated with Fluon (BioQuip, Gardena, CA, U.S.A.) to prevent the ants from escaping. Water was provided ad libitum. Although Argentine ants often occur in an interconnected network of nests with millions of workers, the situation replicated here would resemble a smaller nest at the margin or edge of a larger supercolony (Gordon & Heller, 2014).



**Figure 1.** Diagram of the experimental foraging arenas. The location of arenas relative to the colony varied across the three replicates.

Each container was connected to a foraging arena with ad libitum protein-rich food items and to a central staging area. From the staging area, three additional tubes led to arenas that either contained 1, 9 or 25 individual cells (Fig. 1). The location of the arena types varied across replicate nests. Each cell was a small, inverted cup (diameter = 5 cm at the bottom), open at the top to facilitate observation of the ants and coated with Fluon to prevent escape. Any debris or dead ants that collected in the grids were removed, but the cells were not wiped or washed. Therefore, any pheromone marks left by the ants were not removed.

We conducted the experiment in three stages. First, we recorded by scan sampling the number of ants in each cell across the three arenas when no food was ever present in any of the cells (the 'control' period, 26 July – 8 September 2016: 45–67 scans per nest across 44 days). The number of samples varied across nests because they were not all set up simultaneously. On most days the arenas were scanned once, but on some days multiple scans were taken a minimum of 3 h apart.

In the second stage (8 September – 9 November, or across 64 days), we added a small vial of sugar water to one of the three arenas for each colony. Preferences determined before the experiment found that ants always recruited strongly to sugar water when provided. The choice of arena and cell within the arena's grid was randomly determined for each day, with the following constraints: (1) each arena had to receive the food approximately the same number of times, (2) no individual arena could receive food more than 2 days in a row and (3) no individual cell could receive food more than twice (for the 25-grid arena) or three times (for the

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