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Flexibility in collective decision-making by ant colonies: Tracking food across space and time

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ABSTRACT

Deciding which of many available resources to exploit is a problem faced by a range of decentralized biological systems. For example, ants are able to choose between food sources that vary in quality using a chemical trail. This communication system characterized by a strong positive feedback allows a rapid transfer of information and the selection of the best food source. This is true in static environment, where a single, unchanging solution exists. In dynamic environments however such recruitment often 'lock' groups into suboptimal decisions, preventing a response to changes in available resources. Here, we investigate decision-making in a dynamic environment for the greenhead ants (*Rhytidoponera metallica*) which use a non-chemical recruitment. To experimentally test our study species' ability to adapt to changes in their foraging environment, we offered three feeders that changed in quality. At any given time, only one feeder provided high quality food, while the others provided low quality food. Every two hours, the quality of the feeders changed such that the previously high quality feeder became a low quality feeder, and vice versa. We showed that ants were able to track changes in food quality across space and time. By coupling behavioral observations to computer simulations, we demonstrate that selection of food sources relies uniquely on a retention effect of feeding individuals on newcomers without comparison between available opportunities. The elegance of these parsimonious foraging systems is that the collective decision arises from the perception of conspecifics without the need for a leader having a synoptic overall view of the situation and knowing all the available options.

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1. Introduction

Many group living animals communicate about the location of food sources. Such communication is especially beneficial when food sources are ephemeral or hard to find [1,2], or when they are too large to be exploited by a single individual [3]. The best-known examples of food recruitment are found in the social insects: ants, termites and some species of bees and wasps which have evolved to acquire a wide range of signaling mechanisms [4]. For example, ants, termites and stingless bees mark the route between their nest and discovered food sources with a chemical (pheromone), indirectly leading nestmates to the food. Pheromone trails can enable a rapid mass recruitment to food discoveries, but they also impose constraints on the overall foraging efficiency of a species [5].

It is currently agreed upon that many species using pheromone trails are unable to adapt to dynamic environments, such as switching to exploiting a newly discovered high-quality food source when the foraging effort of the colony is already concentrated on a food source of lesser value [6]. The apparent inability of a group of animals to adapt to changing conditions is supported by laboratory experiments [7–9] and mathematical mean field type models or Monte Carlo simulations [7,10–12]. For example, Beckers et al. [13] first provided black garden ants (*Lasius*

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niger) with a poor quality food and after some time introduced a second, high quality food. When the high quality food was added after the ants had established their trail to the poor quality food, the majority of ants continued to forage on the poor quality food. Mathematical models predict that ants will remain on an established trail for periods longer than the evaporation rate of the pheromone because ants continue to reinforce the trail leading the poor quality food [7,10,14]. Pheromone trails can thus result in ants being "trapped" in suboptimal solutions. Such situations have also been observed in other species using pheromones like stingless bees (Trigona recursa) [15] or caterpillars choosing balanced foods [16]. Other studies [17,18] reported that the ability to allocate or reallocate most individuals on the best food source is dependent on the strength of the positive feedback. Nicolis et al. [17] argued that a system possessing a high nonlinearity is more susceptible to be trapped in a suboptimal solution because of the possibility of the coexistence between two modes of exploitation while a linear or weakly nonlinear system will always select the best food source but in a weaker proportion.

That being said, there are ways to escape the deadlocks of suboptimal solutions. First, a combination of different pheromones allow ants to remember routes to sites that were previously rewarding and may become rewarding again in the near future, allowing the colony to track changing foraging conditions [19,20]. Second, species using positive feedback loops channeled by direct interactions such as contact instead of pheromones are more flexible and prevent the colonies from locking to poor choice [2,21].

In all these species cited above, individuals that discover a food source convey signals to their congeners and trigger the onset of a recruitment process. The foraging behavior of recruited individuals is then influenced by positive feedbacks enhanced by chemical or tactile signals (e.g. pheromone trail, contacts), leading progressively to the collective exploitation of the food sources [22]. A few studies nevertheless suggest that even in the absence of complex recruitment processes, group decisions could rely on non-linear dynamics based on social amplification [16,23,24]. For example Lihoreau et al. [24] reported a collective foraging decision in the gregarious cockroach *Blattella germanica* and describes a foraging decision-making mechanism based uniquely on a retention effect without requiring active recruitment. Their experiments demonstrate that feeding cockroaches recruit 'passively' at the food source without the necessity of active signaling through pheromonal emission or recruitment behavior. All individuals explore their environment randomly and select a resource in relation to the number of conspecifics already on it, thus triggering a positive feedback that leads to collective food selection. In this paper we suggest that these type of decision making process allow more flexibility in changing environment where food source may appear or disappear.

To validate our hypothesis we consider ants that do not use either contacts or pheromone – the greenhead ants *Rhytidoponera metallica*. We study their ability to adapt to dynamically changing foraging conditions. First, we describe experiments showing that green-headed ants are able to quickly adapt their foraging behavior according to changes in food quality. Then, based on feeding behaviors measured at the individual level (time spent feeding according to presence of neighbors), we propose a model to assess the flexibility of collective decision in a dynamic environment.

2. Method

The ponerine ant genus *Rhytidoponera* also named greenhead ants is distributed throughout Australia and its neighboring islands. Colonies of *R. metallica* are found under rocks, in decaying logs, or in leaf-litter and superficial layers of soil [25,26]. In *R. metallica*, nest founding occurs mainly by budding [25] and is associated with the usual presence of multiple fertilised egg-laying workers (gamergates) in the colony [26]. As with most ponerines, workers are monomorphic [25].

Fifteen colonies of *R. metallica* were collected in March 2008 in Sydney, Australia. We collected 1000 ants per mother colony and housed them in a plastic box (l = 20, w = 15, h = 5 cm) the bottom of which was covered by a layer of cotton. The box was connected to a foraging arena l = 40, w = 25, h = 20). The nests were regularly moistened and the colonies were kept at room temperature (25 ± 1 °C) with a 12:12 L/D photoperiod. We supplied ants with water and a mixed diet of vitamin-enriched food [27], as well as drosophila, two times a week.

Before the experiment, the colonies were starved for five days. The experiment started when the ants were given access to a foraging arena (110 cm diameter) placed over the colony. The ants had access to the center of the arena via a wooden stick. We placed two poor and one high quality feeders in the arena 10 cm from the boarder. We used sugar syrup solidified with agar (high quality = 10%, low quality = 2%) as our feeder to allow a better access to the food. Using liquid food promoted crowding at the feeder.

The experiment consisted of two spatial configurations, each performed with one particular type of feeder

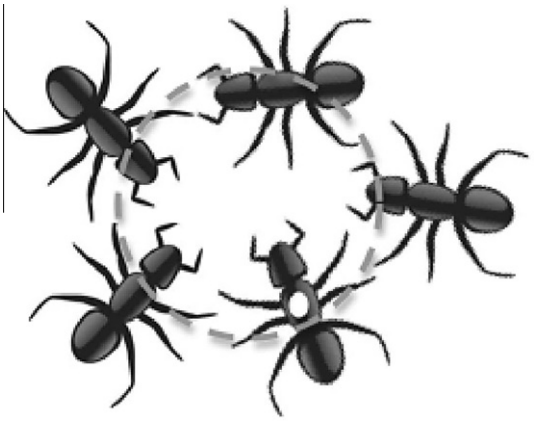

Fig. 1. Focal ant (ants with a white spot) surrounded by four neighbors while feeding.

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