Animal Behaviour 85 (2013) 637–643

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Keeping track of changes: the performance of ant colonies in dynamic environments

Tanya Latty*, Madeleine Beekman

Behaviour and Genetics of Social Insects Lab and Centre for Mathematical Biology, School of Biological Sciences A12, University of Sydney, NSW, Australia

ARTICLE INFO

Article history:
Received 12 March 2012
Initial acceptance 24 May 2012
Final acceptance 21 December 2012
Available online 30 January 2013
MS. number: 12-00190R

Keywords:
Ant
Aphaenogaster longiceps
dynamic foraging
exploitation–exploration trade-off
foraging
group size
Notoncus ectatomoides
Paratrechina longicornis
Pheidole megacephala
Rhytidoponera metallica

Animals living in dynamic foraging environments are subject to trade-offs between exploiting current resources and exploring alternative resources. Social insects face the additional challenge of redistributing an often large foraging force among multiple patches in the absence of leadership or centralized control. We used comparative, field-based techniques to study the dynamic performance of five ant species. We also investigated how the number of ants involved in the decision-making process influenced feeder exploitation and dynamic performance. Colonies were offered two feeders that differed in quality. After 30 min, the feeders changed quality; the challenge for the colonies was to reallocate foraging effort following the swap. We predicted that colonies that invested heavily in exploiting the high-quality resource would have difficulty reallocating foragers following the quality swap. We also predicted that larger foraging groups would have stronger exploitation intensity and better dynamic performance than smaller groups. Overall, we found evidence for a trade-off between exploitation and flexibility such that species that tended to focus strongly on high-quality resources had relatively poor dynamic performance. Contrary to our prediction, we found no evidence that the number of ants influenced dynamic performance. The number of ants did, however, influence exploitation intensity such that colonies with fewer foragers tended to allocate a greater proportion of ants to the higher quality feeder than larger colonies. Our results highlight the factors that influence how species respond to the exploration–exploitation trade-off when faced with short-term fluctuations in the foraging environment.

Animals foraging in patchy environments face the challenge of allocating foraging effort among patches that vary in quality. Allocation of foraging effort can be complicated by the dynamic nature of many environments, where the quality of patches can change as a result of depletion, competition, intrinsic factors and environmental conditions. Individuals in dynamic environments can benefit from allocating a proportion of their time to exploring and monitoring alternative food sources (Kramer & Weary 1991); this leads to a classic trade-off between exploration and exploitation, since any time devoted to exploration of new food sources necessarily takes away from time spent exploiting a known resource. Trade-offs between exploitation and exploration have been studied in a wide range of organisms including slime moulds, chipmunks and pigeons (Shettleworth et al. 1988; Kramer & Weary 1991; Latty & Beekman 2009).

In individual animals, information from sensory systems, physiological state and memory is integrated by the brain and used to make decisions about how to allocate foraging effort among patches. In social insects such as ants, bees and termites, foraging decisions are made collectively, with information on available resource quality spread among many individually acting foragers. Nevertheless, workforce allocation by social insects is remarkably efficient in static environments; when presented with food sources of different quality colonies have been shown to allocate most of their foraging effort to the most rewarding patch (Verhaeghe 1982; Beckers et al. 1990; De Biseau et al. 1991; Seeley et al. 1991; Sumpter & Beekman 2003). Dynamic environments, however, pose a special problem for social insects since reallocating foragers requires close coordination between partially informed individuals.

We studied forager allocation in ant colonies simultaneously exploiting two dynamic food sources. We were interested in a potential trade-off between the intensity of exploitation and the ability to reallocate the foraging force rapidly. A colony that invests heavily in exploiting a high-quality resource might do so at the expense of monitoring the quality of alternative, lower quality resources. We therefore predicted that species that allocated a large proportion of the foraging force towards exploiting a high-quality resource would have difficulty reallocating their foraging force following a decrease in quality.

We were also interested in the effect the number of foragers might have on exploitation and dynamic performance. When given

---

* Correspondence: T. Latty, Behaviour and Genetics of Social Insects Lab and Centre for Mathematical Biology, School of Biological Sciences A12, University of Sydney, NSW 2006, Australia.
E-mail address: tanya.latty@sydney.edu.au (T. Latty).

0003-3472/$38.00 © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2012.12.027

a choice between two feeders of differing quality, theory predicts that larger groups will tend to allocate a greater proportion of their foraging force to the preferred feeder, while smaller groups will have a relatively weak exploitation response (Nicolis & Deneubourg 1999; Nicolis et al. 2011). Although these predictions were made for trail-laying ants, they could conceivably apply to ants using different recruitment mechanisms. We therefore predicted that group size would have a positive effect on exploitation intensity, such that larger groups would allocate a greater proportion of foragers to the preferred feeder.

Having more individuals involved in the decision-making process could aid dynamic performance by facilitating the rapid spread of information. Larger groups of individuals are thought to be better at tracking changing environments than smaller groups, because information disseminates more rapidly in large groups (Adler & Gordon 1992; Pacala et al. 1996; Beekman et al. 2004). Increased information dissemination is predicted in large groups because the per capita interaction rate of individuals is believed to increase with group size (Pacala et al. 1996). We therefore predicted that larger groups would have better dynamic performance than smaller groups.

We chose to use wild ants, rather than laboratory colonies, as this allowed us to observe behaviour in its true ecological context (for example, natural colony sizes and amount of brood). Previous studies on dynamic foraging have used laboratory colonies (Verhaeghe 1982; Beckers et al. 1990; De Biseau et al. 1991; Dussutour et al. 2009a, b; Reid et al. 2011); while this serves as a useful starting point, it does not give us direct insight into how colonies function in their natural state, and could inadvertently prevent species from using mechanisms that allow dynamic redistribution of foraging effort, for example when laboratory colonies are unusually small.

METHODS

Study Area and Study Species

All experiments were conducted at the Crommelin Research Station in Pearl Beach, NSW, Australia between January and April 2011. Temperatures ranged from 25 °C to 35 °C. The study area was a large grassy field interspersed with trees and shrubs. We studied five species of ant common in the study area: *Aphaenogaster longiceps*, *Notoncus ectatomoides*, *Paratrechina longicornis*, *Pheidole megacephala* and *Rhytidoponera metallica*. These species were selected because they were abundant in the study area, had nests that were easy to locate, and are all opportunistic omnivores that forage primarily on homopteran exudates and dead arthropods.

Pheidole megacephala and *P. longicornis* are known to use trail-based recruitment mechanisms (Witte et al. 2007; Dussutour et al. 2009b). *Rhytidoponera metallica* foragers act individually and do not use pheromone trails, although they may use short-range recruitment mechanisms such as stridulation (Pamilo et al. 1985). The recruitment mechanisms of *A. longiceps* and *N. ectatomoides* have not been documented, but our observations suggest they either forage individually (no recruitment) or use in-nest excitation (T. Latty, personal observation). *Paratrechina longicornis* and *Ph. megacephala* are invasive species with cosmopolitan distributions, while *A. longiceps*, *N. ectatomoides* and *R. metallica* are native to Australia (Shattuck 2000). *Paratrechina longicornis* and *Ph. megacephala* are polydomous and individual nests may be connected to other nests via extensive trail networks.

Tracking a Changing Resource

We studied forager allocation in dynamic environments by presenting colonies with food sources that periodically changed in quality. Each colony was offered a choice between two feeders (35 × 10 mm petri dishes) filled with a liquid mixture of sugar, egg, water and whey protein. This diet provided ants with carbohydrates, lipids and protein, and was attractive to a wide variety of species (T. Latty, personal observations). We placed feeders on separate platforms mounted on top of fluon-coated pillars. The platforms were linked to the focal colony via a 20 cm long bamboo stick placed immediately beside the colony entrance (Fig. 1). We enticed foragers to climb the sticks by coating each stick with a thin layer of concentrated food solution; we then allowed the stick to dry before placing it beside the colony. This treatment stimulated exploratory behaviour, but did not provide appreciable amounts of food. Feeders and nests were shaded from direct sunlight. Throughout the experiment we checked to ensure that foragers were returning to the focal nest, and we used a paintbrush to remove any foragers from nontarget species.

We started the experiment when at least two ants were observed drinking at each feeder. This usually took less than 30 min. We then emptied the liquid from both feeders using a syringe. We refilled the feeders so that one randomly selected feeder contained the food mixture at normal concentration (high quality), while the other contained food that had been diluted with water to 15% its original strength (low quality). We counted the ants feeding on each feeder at 5 min intervals. We were interested in how the number of individuals involved in the decision-making process influenced exploitation intensity and dynamic response. To this end, we defined ‘number of ants’ as the total number of ants foraging on both feeders (number of ants on feeder 1 + number of

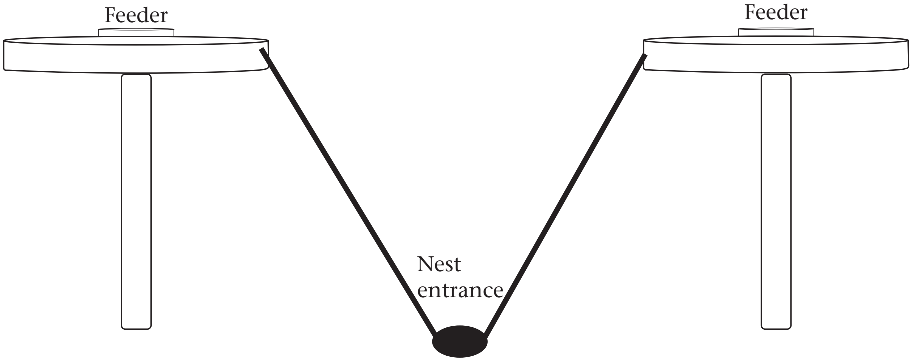

Figure 1. Experimental set-up. Poles were coated with fluon to prevent nonfocal ants from reaching feeding dishes.