

FORAGING ECOLOGY OF THE AUSTRALIAN DESERT ANT *MELOPHORUS BAGOTI*



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TABLE OF CONTENTS

SUMMARY		I
DECLARATION		III
ACKNOWLEDGEMENTS		V

INTRODUCTION		1–10
CHAPTER I	Foraging patterns and strategies in an Australian desert ant	11–32
CHAPTER II	Nest relocation and colony founding in the Australian desert ant <i>Melophorus bagoti</i>	33–46
CHAPTER III	Finding food: outbound searching behaviour in the Australian desert ant <i>Melophorus bagoti</i>	47–84
CHAPTER IV	Finding the nest: inbound searching behaviour in the Australian desert ant <i>Melophorus bagoti</i>	85–110
CHAPTER V	Information content of visual scenes influences systematic search of desert ants	111–138
CONCLUSION		139–146

APPENDIX I	Schultheiss, P., Schwarz, S. & Wystrach, A. 2010. Nest relocation and colony founding in the Australian desert ant, <i>Melophorus bagoti</i> Lubbock (Hymenoptera: Formicidae). <i>Psyche</i> , 2010, 435838. Schultheiss, P. & Cheng, K. 2011. Finding the nest: inbound searching behaviour in the Australian desert ant, <i>Melophorus bagoti</i> . <i>Animal Behaviour</i> , 81, 1031-1038.	147
APPENDIX II	Wystrach, A., Schwarz, S., Schultheiss, P., Beugnon, G. & Cheng, K. 2011. Views, landmarks, and routes: how do desert ants negotiate an obstacle course? <i>Journal of Comparative Physiology A</i> , 197, 167-179.	161

SUMMARY

Melophorus bagoti is a solitary foraging desert ant of Central Australia. As part of a major endeavour to study insect navigation it has recently attracted considerable attention, calling for an intimate knowledge of its foraging ecology. This thesis examines foraging traits on the colony level, and investigates the strategies that are used by foragers when searching for resources. Foraging activity is limited to a window of ca. 50–70°C soil surface temperature, when foragers scavenge opportunistically for food items. Although seemingly capable of laying chemical trails when moving the colony, recruitment behaviour towards large food sources appears to work without the use of pheromone trails. When unable to locate a single target, like a food source or the nest entrance, foragers engage in a systematic search. The size of their search paths is flexible, which allows them to increase search efficiency. To this end, several different cues are used, which inform the foragers of the whereabouts of the target. In food searches, size depends on the type of food, and matches the natural distribution pattern of food items. In nest searches, size depends on the accuracy of the path integrator, which is a navigational tool that accumulates errors. In addition, it depends on the presence of visual navigation cues in the surrounding panorama, and on the amount of information that can be derived from these visual cues. Interestingly, presence or absence of visual cues also changes the movement pattern of searching foragers. Taken together, these results demonstrate how closely searching behaviour is linked with a forager's navigational toolkit, and with its environment.

DECLARATION

I certify that the work in this thesis entitled 'Foraging ecology of the Australian desert ant *Melophorus bagoti*' has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree to any other university or institution other than Macquarie University.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research work and the preparation of the thesis itself have been appropriately acknowledged.

In addition, I certify that all information sources and literature used are indicated in the thesis.

Patrick Schultheiss (Student ID: 41448693)

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From the very first day, Sebastian Schwarz and Antoine Wystrach have been not only colleagues but friends. After 12 months together in the desert, it feels as if they're family and know every side of me (even the strange ones). And I theirs. Seppi must have been the Mum, and his efficient organisation skills proved to be plenty for all three of us. He also supplied us with many delicious meals, and thanks to him I put on weight, despite all the hard fieldwork. Antoine was definitely the kid of the family, as he always had enough energy for all of us. His creative energy helped us all along. I guess that makes me the Dad, whatever that means... Thanks guys, we made a good team.

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INTRODUCTION

'Go to the ant, thou sluggard; consider her ways'

(Proverbs 6:6)

This famous quote from King Solomon is popular with myrmecologists for several reasons. Not only is it evidence that people have been fascinated by ants for millennia, but also that (moral implications aside) important lessons can be learned simply by observing and 'considering' their behaviour. Outside of its original, religious context it can also be seen as an ancient realisation that organisms do not act in isolation, but in the context of their environment.

Aboriginal people of Australia have come to the same conclusions in equally ancient times. In the arid regions of Central Australia, they have considered the ways of ants to such a degree that they have learned to use them to their advantage. Some species of ants, e.g., *Camponotus inflatus* but also *Melophorus bagoti*, which we study here, have a specialised worker caste that can store sugary liquids in their hugely distended abdomens. These workers, the so-called 'honey pots', serve as food storage vessels for the whole colony. Aboriginal people have learned about the ecology and behaviour of these ants, in order to locate and unearth the colonies and collect these ants for food (Conway 1990, 1991, 1992).

Scientists of the modern era have been considering ants since the works of Gould (1747) and Latreille (1802). Since then, they have proven to be an exceptionally diverse group of insects, inhabiting almost every habitat from rainforests to deserts. Despite the relative simplicity of their physiology ants display an astonishing range of often very complex behaviours, making them prime study animals for topics of behavioural ecology and comparative cognition (Wehner 2003).

Navigation in Ants and the Relevance of Ecology

One such topic that has been thoroughly investigated in ants over the last decades is spatial navigation. Much of an ant's lifetime is spent inside the nest, where she performs duties such as brood-rearing, construction and cleaning. Only at the end of her lifetime does she venture outside of the nest to perform the dangerous task of collecting food for the colony (Hölldobler & Wilson 1990). These foragers need to perform two main tasks that require navigational skills: they need to find the food, and they need to bring it back to the nest. Many species of ants reduce the navigational requirements of single foragers by putting up 'signposts' that guide their movements. With the use of pheromones, chemical trail systems are marked out on the ground. These trails can lead foragers from the nest entrance to a profitable foraging area, and also back to the nest. Another process by which fellow ants are guided is recruitment behaviour. If foragers chance upon a large food source that needs to be exploited fast, they can communicate its location, again often involving pheromones, to their nestmates (Hölldobler & Wilson 1990).

However, not all ants make use of these 'guiding mechanisms'. Thermophilic desert ants inhabit hot and arid environments where they occupy the ecological niche of diurnal scavengers. In different parts of the world, desert ant species belong to different genera: *Cataglyphis* in North Africa and Eurasia, *Ocymyrmex* in southern Africa, *Melophorus* in Australia, and *Dorymyrmex* in South America. These ants make little or no use of pheromone trails for foraging because volatile chemicals would evaporate too fast on the hot desert ground, and because food items are randomly scattered and not concentrated into profitable foraging areas (Wehner et al. 1983; Schmid-Hempel 1987). Instead, foragers venture out of the nest solitarily, and therefore display sophisticated navigational skills. Two main mechanisms of navigation, both relying on vision, have been identified: path integration and visual navigation (Wehner et al. 1996; Wehner 2003). In path integration, the running ant uses a step-counter (odometer) to keep track of the distances it runs and celestial visual cues (compass cues) to keep track of the directions it takes. At the end of the journey it is then able to return to the starting point in a straight line. In visual navigation, terrestrial visual cues (landmarks) are used. Desert ants of the genera *Cataglyphis*, *Ocymyrmex* and *Melophorus* are known to use both path integration

and visual navigation (Wehner et al. 1996; Narendra 2007; Wehner & Müller 2010). The relative importance of each strategy, however, largely depends on the complexity of their visual environment. *C. fortis*, for example, lives in an almost featureless salt-pan habitat; its foragers rely mostly on path integration (Ronacher 2008). *M. bagoti*, on the other hand, inhabits semi-arid deserts with many grass tussocks and bushes. As these provide ample landmark cues, its foragers are mainly visual navigators (Cheng et al. 2009). The exact navigational strategies of a given species are therefore deeply entwined with its foraging ecology. In *Cataglyphis*, which has been researched for decades, the ecology of several species is well understood. *M. bagoti*, however, is a more recent addition to the field of ant navigation, and several questions remain open in regard to its foraging ecology.

When Navigation Fails: Searching Behaviour

While navigating, a forager may not immediately find the target it is looking for, e.g., a food source or the nest entrance. Any navigational process is prone to errors, and the animal may not find itself exactly at the position it was aiming for. Alternatively, the target may have changed position or vanished altogether, as when a food source is depleted. In these cases the ant will engage in searching behaviour as a 'back-up' mechanism.

Many studies have focussed on theoretical issues of searching behaviour, often in the context of foraging where several targets are involved (Stephens & Krebs 1986; Ydenberg et al. 2007). Considering that searching incurs costs, e.g., energy and time consumed, an animal is thought to search in a manner that maximises its encounter rate with the target resource (Bell 1990). Using simulations, optimal search strategies can then be identified for the location of targets with different distributions. A crucial part of these considerations is the knowledge the animal has about the resource location (Bell 1991). An ant forager may know very well where its nest is located, but in foraging it may be revisiting a known food source or looking for new, unknown food sources. Similarly, an ant may be more certain or less certain about a given target location, depending on its previous experiences (see for example Merkle et al. 2006). An efficient search strategy will incorporate all these parameters into the structure of the search path, optimising the target encounter rate.

In the context of navigation, the exact structure of an ant forager's search path can therefore inform us about its current knowledge. This in turn may give us insight into how navigationally relevant information is processed, both when locating a food source and the nest entrance.

The Study of Melophorus bagoti Desert Ants

After the initial species description by Sir John Lubbock (Lubbock 1883), the Red Honey Ant *Melophorus bagoti* was encountered on scientific expeditions to Australia (e.g., Froggatt 1896; Forel 1915), but apparently not further studied until the 1990s. While its behavioural ecology is now sufficiently understood to confirm the ecological equivalence with thermophilic ants of the genus *Cataglyphis* (Christian & Morton 1992; Wehner et al. 2003), only a single study has so far explicitly investigated its foraging ecology, focussing on individual-level traits (Muser et al. 2005). Since then, an increasing amount of research has explored the navigational and cognitive abilities of *M. bagoti* (e.g., Cheng et al. 2006; Narendra et al. 2007a; Narendra et al. 2007b; Graham & Cheng 2009; Schwarz & Cheng 2010; Schwarz & Cheng 2011; Wystrach et al. 2011).

Research Objectives

This thesis deals with two main aspects of foraging ecology in *M. bagoti*. They both investigate fine-scale influences of environment on behavioural patterns of foragers. The first part, comprising the first two chapters, explores colony-level traits, with special emphasis on seasonal variation and pheromone use. These topics are of special interest, as they could have implications for navigational studies on this species of desert ant. The remainder of the chapters examines the strategies that are used by foragers to locate resources such as a food source or the nest entrance. Their searching behaviour was studied in various contexts, showing what environmental cues are used to inform foragers about the location of these targets.

This work highlights the adaptive flexibility of ant behaviour. It will be of interest not only for future studies on navigational and cognitive abilities of desert ants, but also for researchers in the fields of optimal searching theory and foraging theory.

Thesis Organisation

Chapter I investigates colony-level foraging activities. Foragers are shown to be true scavengers, with diet composition varying considerably and depending on seasonal availability rather than strict preferences. They are also capable of recruiting nest-mates to profitable food sources, which is very unusual for thermophilic desert ants. This chapter is submitted to *Austral Ecology*. It is co-authored by Sabine Nooten, who helped with data collection and analysis, and provided comments on the manuscript (my contribution to experimental design: 90%; data collection: 80%; data analysis: 70%; writing: 90%).

Chapter II contains observations on nest relocation behaviour and the founding stages of new colonies. While not strictly concerned with foraging ecology, it provides details on the use of pheromone trails, which are used to guide colony members to the new nest site. Such a chemical guidance mechanism may also be employed in a foraging context. This chapter has been published in *Psyche: A Journal of Entomology*. It is co-authored by Sebastian Schwarz and Antoine Wystrach, who contributed to the data collection and provided comments on the manuscript (my contribution to data collection: 70%; writing: 90%; as this chapter does not have an experimental component, the categories 'experimental design' and 'data analysis' do not apply here).

Chapter III investigates the strategies by which foragers locate previously visited food sources. By looking at search paths of foragers in detail, it could be shown that they used the same general search strategy for finding two different types of food, but that the strategy was then fine-tuned to specific food qualities. This chapter is published in *Behavioral Ecology*. It is co-authored by Ken Cheng, who commented on the manuscript (my contribution to experimental design: 100%; data collection: 100%; data analysis: 90%; writing: 90%).

Chapter IV focuses on the strategies that are used to find the nest entrance after successful foraging trips. These were studied in a distant test field that was devoid of familiar visual landmark cues. In this context, where visual navigation is not viable, foragers adjusted their search path to incorporate the cumulative error of path integration. Model fitting revealed that their search strategy appears as a composite of two separate strategies. This chapter is published in *Animal Behaviour*. It is co-authored by Ken Cheng, who provided suggestions to the experimental design and commented on the manuscript (my contribution to experimental design: 80%; data collection: 80%; data analysis: 80%; writing: 90%).

Chapter V further explores the strategies used for finding the nest entrance. Here, foragers were studied as they displayed searches at the actual nest site, where all familiar visual cues were present. Model fitting revealed a different search strategy to that used in a distant test field, demonstrating the importance of familiar visual cues. Additional manipulations of the visual environment around the nest showed that foragers make use of as much visual information as possible. This chapter is submitted to *The Journal of Experimental Biology*. It is co-authored by Antoine Wystrach and Eric Legge, who contributed to all parts of the study, and by Ken Cheng, who provided comments on the manuscript (my contribution to experimental design: 50%; data collection: 60%; data analysis: 70%, writing: 80%).

A general **Conclusion** brings together the main findings from the separate chapters and provides ideas and suggestions for further studies.

Appendix I contains Chapters II and IV in their published format:

- Schultheiss, P., Schwarz, S. & Wystrach, A. 2010. Nest relocation and colony founding in the Australian desert ant, *Melophorus bagoti* Lubbock (Hymenoptera: Formicidae). *Psyche*, 2010, 435838.
- Schultheiss, P. & Cheng, K. 2011. Finding the nest: inbound searching behaviour in the Australian desert ant, *Melophorus bagoti*. *Animal Behaviour*, 81, 1031-1038.

Appendix II contains a paper to which I contributed during my PhD candidature. Its topic is related to that of the thesis and deals with route following behaviour of foragers on their way from a familiar food site to the nest entrance.

- Wystrach, A., Schwarz, S., Schultheiss, P., Beugnon, G. & Cheng, K. 2011. Views, landmarks, and routes: how do desert ants negotiate an obstacle course? *Journal of Comparative Physiology A*, 197, 167-179.

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CHAPTER I

Foraging patterns and strategies in an Australian desert ant



This chapter is submitted to *Austral Ecology*

Foraging patterns and strategies in an Australian desert ant

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Abstract

Melophorus bagoti is a thermophilic, solitary foraging desert ant that inhabits the semi-arid regions of Australia. In recent years, it has become a model species for the study of navigation. However, its ecological traits are poorly documented, especially on the level of the entire colony. Here, we investigated this species' daily activity schedule and diet composition, and examined its foraging behaviour. Foraging activity is confined to a window of roughly 50–70°C soil surface temperature, and foragers react quickly to temperature changes. Consequently, the daily activity pattern during summer is unimodal on warm days and bimodal on very hot days. Foragers are opportunistic scavengers; dead insects make up a large proportion of collected food items, but grass seeds are also occasionally collected in large amounts. Diet composition changes with the seasonal availability of certain food groups. Unusual among thermophilic desert ants, *M. bagoti* foragers have the ability to recruit nestmates to profitable food sources. Recruitment seems to function without the use of pheromone trails, but the exact mechanism requires further investigation.

Keywords: Desert ant – foraging ecology – foraging patterns – diet – scavenger – recruitment

Introduction

Deserts all over the world provide a unique and special habitat for animals. Thermophilic desert ants are superbly adapted to the hot and dry conditions, and several species have evolved in different parts of the world. It has been hypothesised that these species occupy equivalent ecological niches, and that each continent has its 'own' thermophilic desert ant (Wehner 1987). So far, these have been identified in the genera *Cataglyphis* in Eurasia and northern Africa (Wehner et al. 1983), *Ocymyrmex* in southern Africa (Marsh 1985a), *Dorymyrmex* in South America (Goetsch 1935) and *Melophorus* in Australia (Briese & Macauley 1980, 1981).

These ants are strictly diurnal, solitary foraging scavengers, and several species are inactive over the cooler winter period. Their thermophilic lifestyle is reflected in morphological, physiological and behavioural adaptations (Cerdeña & Retana 2000; Cerdeña 2001). Foragers have very long legs, raising the body into cooler air layers above the ground and enabling high running speeds (Sommer & Wehner 2012). They can withstand very high temperatures (Marsh 1985b; Christian & Morton 1992; Wehner & Wehner 2011), possibly due to special patterns in the synthesis of heat shock proteins (Gehring & Wehner 1995). This enables them to prey on other insects that have succumbed to the heat while also avoiding competition with other ant species (Briese & Macauley 1980) and predation (Wehner et al. 1992). As they are often active at temperatures close to their critical thermal maximum, they make extensive use of thermal refuges in their habitat, where they are able to lower their body temperature slightly (Marsh 1985a; Christian & Morton 1992).

Dead insects are randomly distributed in space, and to scavenge efficiently, desert ants are solitary foragers (Wehner et al. 1983; Schmid-Hempel 1987). As such, each individual ant needs to be able to navigate within its environment, and find the way back to the nest. Desert ants have developed several highly sophisticated mechanisms with which to accomplish these tasks, and have therefore become model organisms for the study of navigation (Wehner 2003, 2008; Cheng et al. 2009). *Cataglyphis* ants have been at the forefront of navigational research for several decades (reviewed in Wehner 2003), and many studies have shown that their physiology and behaviour are finely attuned to their specific ecological constraints. In

this respect, comparisons of species from different desert habitats have been particularly revealing. As such, the Australian desert ant *Melophorus bagoti* has attracted increasing attention in recent years (reviewed in Cheng et al. 2009).

Navigational strategies and cognitive abilities of different desert ants can only be fully understood with reference to the ecology of the given species. However, our knowledge about the ecology of *M. bagoti* is sparse, and only a handful of studies provide details. On the individual level, Muser et al. (2005) have investigated the ontogeny of foraging behaviour in detail. On the colony level, studies have described the nest architecture (Conway 1992) and nest relocation behaviour (Schultheiss et al. 2010), and we have some limited information on daily diet and activity (Christian & Morton 1992; Muser et al. 2005). With this study, we extend this knowledge by looking at diurnal activity profiles and diet composition of *M. bagoti* in detail, and discuss causes of variation. Further, we experimentally address whether foragers are able to recruit nestmates to profitable food sources. So far, *M. bagoti* is regarded as an entirely solitary forager, where each individual ant navigates alone. It is important to investigate the possibility of communal foraging strategies, as these may interact with the navigational strategies of individual foragers.

Material and Methods

The study site is located ca. 10 km south of Alice Springs, Central Australia. The area is characterised by semi-arid climate, and the vegetation is dominated by tussocks of Buffel grass *Cenchrus ciliaris*, interspersed with *Acacia* and *Hakea* bushes and the occasional large *Eucalyptus* tree. Nests of *M. bagoti* occur at a density of ca. 3 per ha. They are completely underground, and usually have only one entrance.

Foraging activity was monitored during the summer season (November to January) at three different nests. Over a complete day, the number of outbound foragers was noted in 5 min periods (local time; the time series was later adjusted to solar time, rounded to the closest 5 min period). All outbound ants that traversed a circle of 1 m radius around the nest and did not carry any visible items were counted as foragers. Temperature of the sun-exposed soil surface was measured in close

vicinity of the nest entrance every minute with a data logger (Onset[®] Hobo U12-013). The thermocouple was placed directly on the ground and covered with a thin layer of sand.

Diet composition, excluding liquid food intake, was assessed at three different nests. At each of these, three samples were taken at different time periods of the same season: in the early foraging season (26 November to 01 December 2009), at the peak of the season (17 to 21 January 2010), and late in the season (20 to 22 February 2010). Early samples were also collected in a second season at different nests (16 to 19 December 2008). Early samples were also collected in a second season at different nests. All samples were taken over one full foraging day or two days if the number of food items was low (< 50 per day). All returning successful foragers were intercepted, and their food items classified into broad categories, including insect and plant items. Insects, which comprise a large part of their diet, were categorised according to their taxonomic order. Diet composition was then compared between (a) nests, (b) seasonal periods, and (c) years using the PERMANOVA+ add-on package (Anderson et al. 2006) for the statistical software programme Primer v6 (Clarke & Gorley 2006). Following suggestions from Warton & Hui (2011) we used logit instead of the more widely applied arcsine transformation, as this delivers improved statistical power for comparisons of proportional data. The transformed proportional data were used as the base for Euclidean distance matrices, followed by a one-way permutational MANOVA or PERMANOVA (Anderson 2001).

The question of recruitment was addressed experimentally. If recruitment occurs, a previously visited food source will be visited by more newly arriving foragers than a new, not previously visited food source. At two nests, feeders (small plastic containers) were sunk into the ground at a distance of 3 m from the nest entrance. Four feeders were installed at each nest, located at the main compass directions (N, E, S, and W). The walls of the feeder were coated in Fluon[®] (Asahi Glass Company), so that ants in the feeder were not able to climb the walls and escape. Activity was monitored at all feeders over three consecutive 15 min intervals, by counting the ants that were trapped in the feeders during that time. All counted ants were then released from the feeders simultaneously. Before each test, baseline activity at the empty feeders was measured (interval 1). After releasing all counted

ants, a large food source (5–7 freshly cut up mealworms) was installed in one feeder (the ‘test feeder’), and again activity was measured at all feeders (interval 2). If activity was low (< 2 foragers in the test feeder), this interval was extended to 30 or 45 min. All trapped ants were again released, and foragers that carried food items from the experimental food source were left to carry it back to the nest. While they returned to the nest, similar sized food sources were quickly installed in the two feeders adjoining the test feeder; the feeder opposite to the test feeder remained empty. Activity at all feeders was again monitored (interval 3). We ensured that food was never placed in feeders that were upwind of the nest entrance, that each nest was tested no more than once a day, and that the direction of the test feeder always changed between tests. The described setup had the effect that during the third interval, the nest was surrounded by one food source that had previously been visited by foragers, and two more food sources that had not been visited yet. Recruitment behaviour will result in a higher number of foragers at the first (known) food source than at the other (unknown) food sources. On the other hand, if no recruitment occurs all three food sources should be visited equally. Chi-squared tests were used to see if forager numbers at the three food sources differed from an equal (chance) distribution.

This experimental set-up was then slightly modified to test if foragers that return from a large food source lay any pheromone trail on their return journey to the nest. A large white sheet (ca. 3×3 m) was placed on the ground around the nest, with a hole in the centre (ca. 15 cm diameter) providing access to the nest entrance. Feeders were placed as before, and activity was again monitored over three 15 min intervals. The first interval measured baseline activity, the second measured activity after instalment of one large food source (as above). After all foragers were released and had returned to the nest, the sheet was lifted and turned by 180° . A second large food source was then placed in the feeder opposite to the test feeder, and foragers in the feeders counted after the third interval. If returning foragers deposit trail pheromones on the ground that guide other ants to the food source, this trail will now point in the opposite direction, and the majority of outbound foragers should now run to the second food source.

Results

Foraging Activity

M. bagoti often closed its nest entrance over night. During summer, the entrance was usually opened at around 9 am, and the first ants emerged from the nest. At most nests, foraging activity began shortly thereafter. Soil surface temperature at onset of foraging was high, but varied considerably ($51.5 \pm 8.4^{\circ}\text{C}$, $n = 11$). On typical, moderately hot days, this activity continued throughout the day until around 5.30 pm (Fig. 1a). When the last foragers left the nest, soil temperatures were still quite high ($49.8 \pm 3.3^{\circ}\text{C}$, $n = 11$). On hotter days, foraging activity slowed down over the midday period, leading to a two-peaked activity pattern (Fig. 1b). On exceptionally hot days, this pattern was much more pronounced, and activity ceased completely for several hours over midday. Overall forager numbers on these days were greatly reduced (compare Figures 1b and 1c, which show the same nest on different days).

However, this activity pattern changed on days with intermittent cloud cover, which are quite common in Central Australia. On otherwise moderately hot days, this led to a reduction in total forager numbers compared to cloudless days (compare Figures 1a and 1d, which show data from the same nest). However, on very hot days cloud shading did not lead to reduced forager numbers (compare Figures 1e and 1f, showing data from the same nest). Instead, activity on the cloudy day was almost entirely restricted to the cooler cloud periods. Also, foragers were active during the midday period, when activity had completely ceased on cloudless hot days.

Diet Composition

Diet composition of three nests over the course of one foraging season is shown in Figure 2 a–c; a summary of statistical results is shown in Table 1. Between nests, diet was very similar, but diet composition varied considerably over the course of the season. Between two consecutive years, diet composition did not differ significantly (measured at early season only, see Fig. 2a and d). A very similar

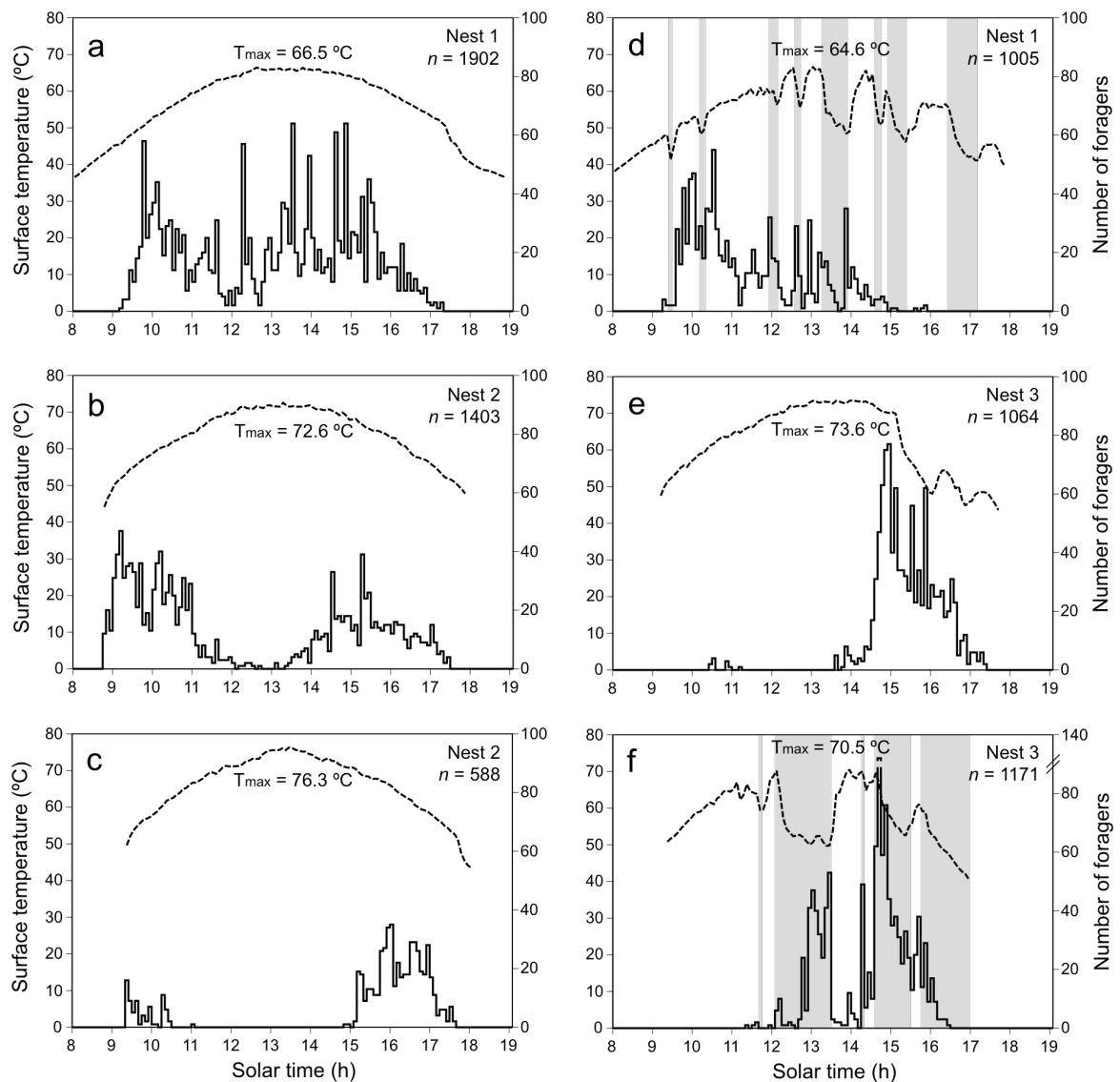


Figure 1: Foraging activity patterns during summer at three nests of *M. bagoti*. Dashed lines show soil surface temperature (left ordinate), and stepped lines show the number of outbound foragers (right ordinate) every 5 min. Grey bars indicate shading of the nest entrance by passing clouds. The maximum observed surface temperature (T_{max}), nest number, and n -values are given in each panel. (a)–(c) Activity on cloudless days, shown for a moderately hot (a), a hot (b), and an extremely hot day (c); data in (b) and (c) were collected at the same nest. (d) Activity on a moderately hot day with intermittent cloud cover, measured at the same nest as (a). (e) and (f) Foraging activity patterns taken at the same nest on hot summer days, without any cloud cover (e), and with intermittent cloud cover (f). Data were collected on (a) 10.01.09, (b) 22.01.10, (c) 16.11.09, (d) 04.01.09, (e) 27.11.09, and (f) 18.11.09.

pattern emerges if only the insect portion of the diet is considered. Here, diet composition was very similar between nests but significant changes occurred over the season. Also, there were no significant differences between years.

Table 1: Summary of PERMANOVA results for the overall diet composition (top) and the insect proportion only (bottom); see Figure 2

Factor	df	Pseudo- <i>F</i>	<i>p</i> (perm)
overall diet composition			
Nest	2,6	0.21	0.991
Season	2,6	4.08	< 0.01
Year	1,4	5.39	0.010
insects only			
Nest	2,6	0.14	0.997
Season	2,6	8.39	< 0.01
Year	1,4	4.26	0.199

Desiccated insects or insect parts made up a large proportion of the diet. These were mainly of the orders Hymenoptera, Orthoptera, Lepidoptera, and Hemiptera (Fig. 2). Foragers of *M. bagoti* scavenged for these food items, and did not actively hunt insects. Occasionally, considerable amounts of plant material were also collected. For the most part (> 95%), this was comprised of seeds of the Warrego summer grass *Paspalidium jubiflorum*. Only a very small portion from the base of the seeds (the lower glumes) was retained in the nest, and the rest of the seed discarded. During the foraging season, diet composition changed in the following manner. In the early season, much of the diet consisted of insects (mostly Hymenoptera, Orthoptera, and Hemiptera), and only small amounts of plant material were collected (Fig. 2a). At the peak of the season, the proportion of Hymenoptera was reduced, and that of Lepidoptera and plant material increased (Fig. 2b). Toward the end of the season, foragers collected much larger amounts of plant material. Insects were now mostly of the orders Hemiptera and Lepidoptera, and the proportion of Hymenoptera was very small (Fig. 2c). Diet in the early season was also sampled during a second season, where proportions of food items were slightly different. Foragers collected an increased amount of plant material, and a smaller proportion of Hymenoptera (Fig. 2d).

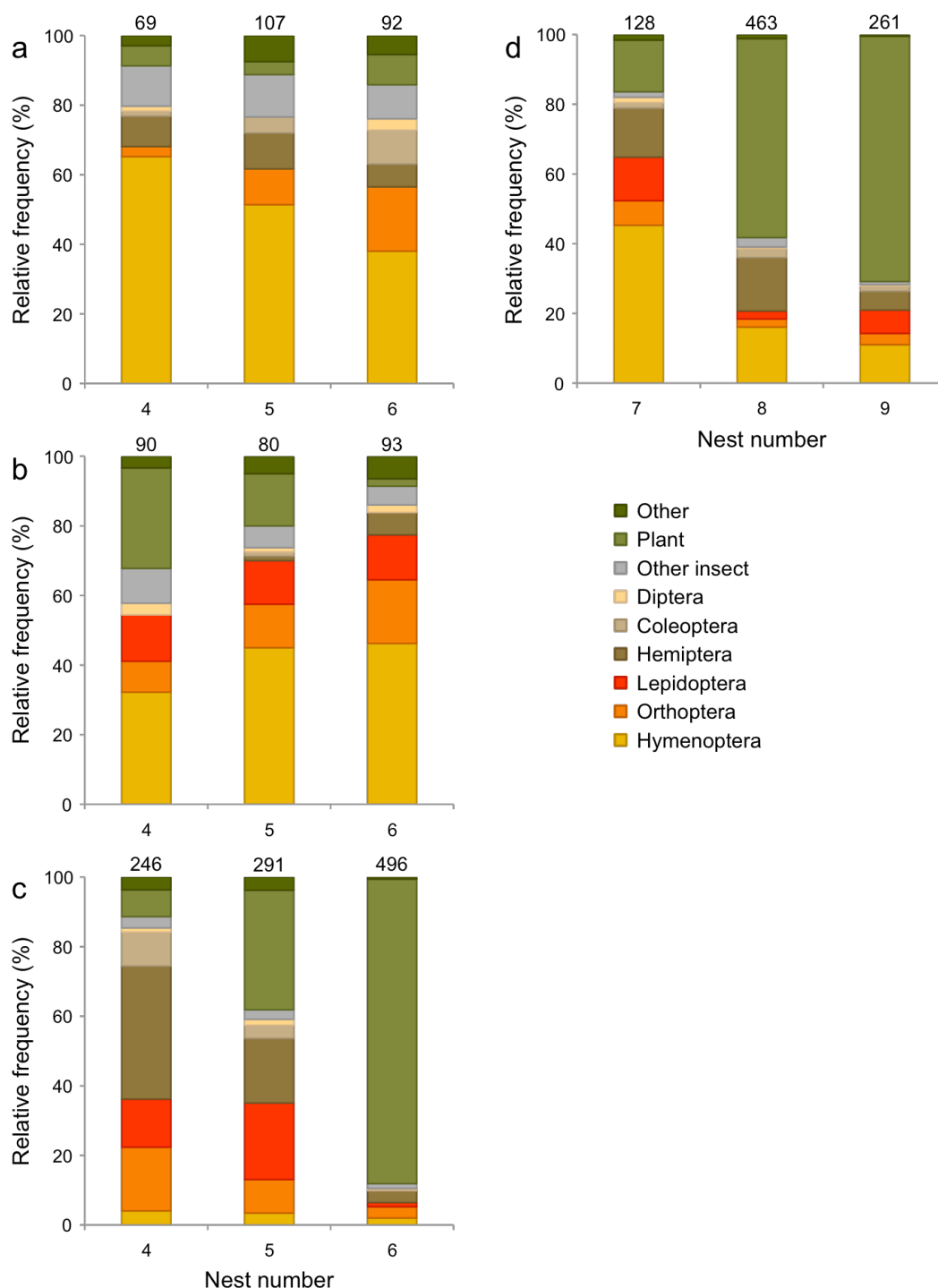


Figure 2: Diet composition of *M. bagoti*, measured as relative frequency of food items in 9 different categories; numbers show *n*-values. (a)–(c) Composition of diet of three nests, each sampled three times during the summer foraging season 2009/2010: early in the season (a), at the peak of the season (b), and late in the season (c). (d) Early season sample from a different year (2008), taken at three different nests.

In addition to food items that were carried back to the nest, a small number of foragers regularly collected sugary plant secretions. For the most part, these came from the bark of River Red Gums *Eucalyptus camaldulensis*, but also from the flowers of *Zaleya galericulata* and *Hakea eyreana*. In some cases, the sugary secretion had dripped onto the ground and dried, and the foragers carried away small stones and twigs that were covered in it. These items make up most of the 'other' category.

Recruitment

Results of the recruitment experiments are shown in Figure 3. In all experiments, baseline activity at all feeders was very low. Installing a food source in one of the four feeders increased the number of foragers at that feeder slightly. In four instances (all at the same nest), return of these ants to the nest with their food items resulted in very high activity at the test feeder shortly afterwards; forager numbers increased about tenfold (Fig. 3a). The number of foragers at the other feeders was slightly increased, but remained much lower. In all four runs of the experiment at this nest, forager numbers differed significantly from the chance distribution ($\chi^2(2)$: 124.4, 118.9, 114.7, 89.9; all $p < 0.001$). This response is consistent with recruitment behaviour. In four other instances (all at a second nest), return of the foragers did not elicit any change in foraging activity (Fig. 3b). The number of foragers that returned to the nest with food items was generally lower than at the first nest, but there was some overlap. Laying down a sheet on the ground and turning it by 180° after returning foragers had entered the nest did not change the recruitment response. Foragers were still recruited to the first food source, and not in the opposite direction (Fig. 3c). Also, in all the experiments returning foragers were never seen actually touching the ground with the tips of their abdomens, a behaviour which would presumably be necessary for laying odour trails.

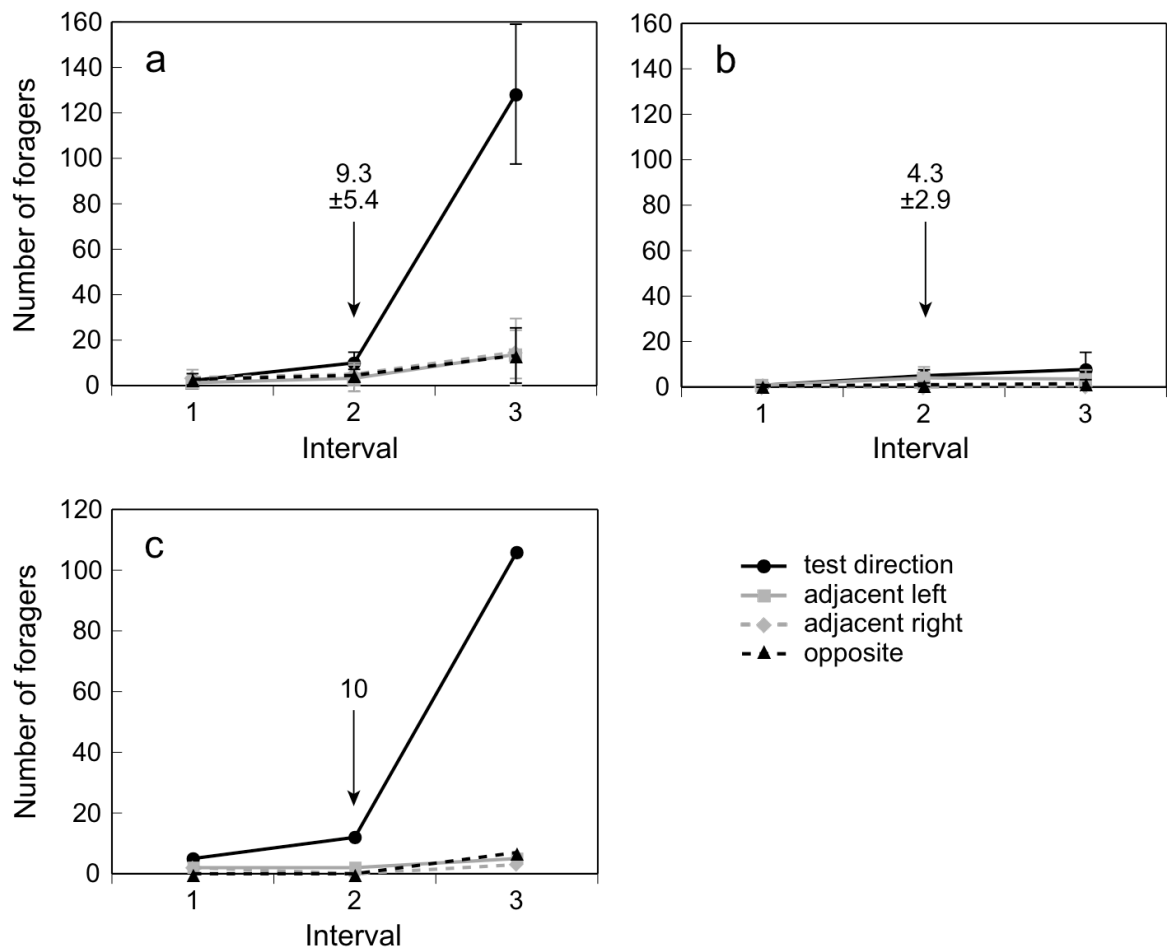


Figure 3: Recruitment responses in *M. bagoti*, measured at four feeders as shown in legend. Numbers show count of foragers that returned to the nest with food, after being released at the end of interval 2. (a) Data from four experimental runs at one nest ($M \pm sd$). (b) Data from four experimental runs at a second nest ($M \pm sd$). (c) Data from a single experimental run, performed at the same nest as (a). Here, a sheet on the ground was turned by 180° between intervals 2 and 3; see text for details.

Discussion

Activity Patterns and Temperature

M. bagoti foragers are active at temperatures that are close to their physiological maximum (Christian & Morton 1992; Wehner et al. 1992; Wehner & Wehner 2011). By avoiding cooler temperatures, they probably reduce interspecific competition and the risk of predation (Muser et al. 2005). On most summer days, foragers start leaving the nest if soil temperatures are sufficiently high (ca. 50°C) and activity continues throughout the day (Fig. 1a). There is, however, considerable variation in their daily activity patterns, and it appears that foraging activity is not only limited by low, but also by high temperatures. Generally, foraging activity ceases at soil temperatures above ca. 70°C. On hot days, these temperatures are only reached over the midday period, and cessation of activity leads to a bimodal activity pattern (Fig. 1b); this break is longer on hotter days and can last several hours (Fig. 1c). Foraging activity seems to be finely tuned to this 'temperature window': 93.6% of all foragers leave the nest at temperatures of 49–71°C. Foragers react to changes in temperature within minutes, as can be seen on cloudy days. Passing clouds lead to a reduction in solar radiation and an immediate drop in surface temperature. During hot parts of the day when nests were otherwise inactive, this lowered the temperature below 70°C and foragers resumed their activity (Fig. 1f). When cloud cover reduced the temperature to below 50°C, however, activity was much reduced (Fig. 1d). Previous studies have shown temperature-dependent activity rhythms for several species of *Cataglyphis* and *Ocymyrmex* desert ants. In a similar fashion, these ants displayed unimodal activity patterns on cooler days and bimodal patterns on hotter days (Marsh 1985a; Wehner & Wehner 2011).

Although activity at the nest ceased at soil temperatures of 70°C or above, foragers outside of the nest often remained active to some degree. At these hot periods, air temperature at ant height is close to the thermal maximum of *M. bagoti*, and foragers increasingly engage in respite (cooling-off) behaviour (Christian & Morton 1992; personal observation). They seek out and spend some time in cooler

microclimates, i.e., they climb up blades of grass or twigs, or move into patches of shade. Even though these refuges are often very small and foragers only spend short times in them, this lowers their body temperature sufficiently for them to continue foraging.

Diet Composition over the Season

Foragers of *M. bagoti* are generalists, and they exploit a diverse range of food types. Many of the items carried back to the nest consisted of different kinds of insects (Fig. 2), which is consistent with results reported by Muser et al. (2005). During the same seasonal period, different nests tended to collect similar proportions of food items. However, these proportions changed over the course of the season. Thus, *M. bagoti* foragers seem to be opportunistic scavengers; their diet composition appears to depend less on preference, but more on the availability of food items at different times of the foraging season. As food items that are obtained by scavengers are usually unpredictable in food value, quantity, and location (Carroll & Janzen 1973), it seems that scavenging foragers need to be opportunistic to ensure a sufficient supply of energy. Opportunistic strategies are also predicted for foragers in low nutrient environments (Pyke 1984), which appears to be the case for *M. bagoti* (Muser et al. 2005). If the encounter rate with food items is low, foragers should not develop any preferences, but collect all encountered items.

In addition to insect carcasses, some nests also made extensive use of Warrego summer grass seeds as a food source. While several other species of *Melophorus* are known to be seed harvesters (Andersen 2007), *M. bagoti* was thought to make almost no use of plant material apart from sugary excretions (Muser et al. 2005). Unlike true harvester ants which feed on the seed itself (Hölldobler & Wilson 1990), *M. bagoti* consumed only a small part from the seed base and discarded the actual seed. This behaviour is therefore closer to that of ants exploiting myrmecochorous plants, where only a small edible appendage is attached to the seed. After detaching this small appendage the seed is discarded, which aids the dispersal of the plant (Hölldobler & Wilson 1990). Despite being collected in large numbers at times (Fig. 2), these seeds do not form a constant part of the diet of *M. bagoti*; many nests were never observed collecting grass seeds in noticeable

amounts (personal observation). In fact, Warrego summer grass was only common at the study site when precipitation levels were higher than usual for the area, as in December 2008 (Fig. 2d) and in February 2010 (Fig. 2c). Also, this grass was patchily distributed so that some nests had access to the seeds while others did not. While *M. bagoti* makes use of these seeds when available, grass seeds are by no means an essential part of their diet.

Recruitment

Recruitment is a form of communication with which nestmates are led to a certain point in space, e.g., a food source or a nest site (Wilson 1971). During recruitment, information about the location or at least the direction of the target has to be transferred from the recruiting ant to the recruited ant. All recruitment strategies involve chemical communication to some degree, often in the form of odour trails along which recruited ants orient (Hölldobler & Wilson 1990). We performed food recruitment experiments at two different nests. At one nest, when several foragers returned to the nest from a large protein food source in short succession, the colony consistently responded not only with slightly increased general foraging activity but also with a strong directional recruitment response towards that food source (Fig. 3a). At the second nest, no recruitment response occurred (Fig. 3b). This may be due to the lower number of foragers that initially found the food source and returned to the nest with food items, or some other nest-associated factor, e.g., the reproductive state of the colony.

Under natural conditions, foragers of *M. bagoti* rarely encounter large protein food sources, and in many hours of observation recruitment behaviour could never be observed occurring naturally. Dead insects are usually small enough to be carried back by a single forager, and are randomly distributed in space. Carbohydrate food sources are often larger, but are then repeatedly visited by the same forager until depleted. Experimentally, large carbohydrate food sources did not elicit a recruitment response (Muser et al. 2005; personal observation). However, large protein food items can be found occasionally, e.g., a large locust or a lizard. These items cannot be exploited by single ants, making a group effort necessary.

Among thermophilic scavengers recruitment behaviour is exceptionally rare. To our knowledge, it has only been observed in *Ocymyrmex velox* and, in a single instance, in *Cataglyphis bicolor* (Wehner 1987). Strictly speaking, *O. velox* is not a pure scavenger and displays recruitment behaviour only when preying on termite nests. In these cases, single ants recruit small groups of nestmates (5–10 recruits) by depositing pheromone marks on the ground while walking from the nest to the food source. The case of *C. bicolor* refers to an exceptional recruitment event, which occurred when marked foragers were shuttling back and forth between a food source and the nest. A number of unmarked foragers emerged from the nest, and seemed to orient visually towards the returning foragers, which they antennated; they may have used them as a cue for the direction of the food source (Wehner 1987). Apart from this single observation, recruitment has not otherwise been observed in *C. bicolor* (Schmid-Hempel 1987).

What can we deduce about the recruitment strategy in *M. bagoti*? To help answer this question, we will describe a full recruitment response in detail. After the first food source was installed, some foragers found it by chance and were trapped in the feeder (in some cases these foragers were then marked with a spot of paint on their abdomen). Most of these foragers readily picked up a food item and when released, returned to the nest entrance immediately with high running speeds. These foragers were never observed to touch their abdomen to the ground on their return journey, and we also show experimentally that they do not mark the way to the food source by laying an odour trail on their way to the nest (see Fig. 3c). Returning foragers entered the nest in quick succession (at this time two control food sources were installed, see Methods), and about 30 seconds later large numbers of ants surged out of the nest entrance. Some of these went straight towards the first food source but many milled around close to the entrance for some seconds, before moving off in the direction of the test feeder too. On their way to the feeder, the ants formed a wide column and did not follow the same path; their running speeds were as high as on normal foraging trips. In the cases where the recruiting ants were marked (three out of four experimental runs), these were never among the first ants to leave the nest, and they were not followed by distinct groups of recruits. In one instance, only a single ant among 163 recruited ants in the test feeder had previously been marked as a recruiter. Considering these observations, it is very unlikely that

recruiters laid any odour trails on their way from the nest to the feeder, or that they acted as leaders and guided recruits to the food source.

Nevertheless, recruits evidently did receive directional information that led them to the original feeder (Fig. 3a). Conceivably, returning recruiters could have deposited a short trail very close to the nest entrance or even in the entrance hole itself. Such a marking would not be affected by our sheet manipulation (Fig. 3c), and could be used by emerging foragers as a directional cue towards the food source. Alternatively, there could be some kind of information transfer inside the nest. Although clearly requiring further study, we can conclude that recruitment behaviour in *M. bagoti* is different to that of other thermophilic desert ants, and that it may be unusual among ants in general. The ability to communicate food locations to fellow foragers may also be useful in other foraging contexts, and has to be considered in future studies on the navigational abilities of *M. bagoti*.

Conclusion

This study has shown that *M. bagoti* is similar to other thermophilic desert ants in many respects. The activity profiles of nests can vary considerably from day to day, owing to the confinement of activity to a window of ca. 50–70°C soil surface temperature. Foragers are opportunistic scavengers that mostly collect dead insects. But in other regards, *M. bagoti* differs from other desert ants. When available, foragers make extensive use of grass seeds as a food source. They also have the means to communicate the location of food items and retrieve large food sources communally by a group effort. It is likely that these differences arise from their choice of habitat. Compared to most other thermophilic desert ants, *M. bagoti* lives in more complex environments; the surrounding vegetation is comprised of grasses, bushes, and occasional trees. In this environment grass seeds are at times abundant, and large food sources may also be more common. The foraging characteristics of *M. bagoti* seem well suited for this type of habitat.

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CHAPTER II

Nest relocation and colony founding in the Australian desert ant *Melophorus bagoti*



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Nest relocation and colony founding in the Australian desert ant *Melophorus bagoti*

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Abstract

Even after years of research on navigation in the Red Honey Ant, *Melophorus bagoti*, much of its life history remains elusive. Here, we present observations on nest relocation and the reproductive and founding stages of colonies. Nest relocation is possibly aided by trail laying behaviour, which is highly unusual for solitary foraging desert ants. Reproduction occurs in synchronised mating flights, which are probably triggered by rain. Queens may engage in multiple matings, and there is circumstantial evidence that males are chemically attracted to queens. After the mating flight, the queens found new colonies independently and singly. Excavation of these founding colonies reveals first insights into their structure.

Keywords: Desert ant – *Melophorus bagoti* – nest relocation – pheromone trail – nuptial flight – nest architecture

Introduction

The Australian desert ant, *Melophorus bagoti* Lubbock, is a widespread species of arid Central Australia. It inhabits low-shrub and grassland deserts, where it builds fairly large underground nests (Conway 1992). The outdoor activity is mainly restricted to the hotter summer months, when the ants are active during the heat of the day. Foragers usually begin their activity at soil surface temperatures of about 50°C, and continue to forage at temperatures above 70°C (Christian & Morton 1992). They forage solitarily for food such as dead insects, seeds, and sugary plant exudates (Muser et al. 2005; personal observations) and are well known for their ability to store liquids in the abdomens of specialised workers, the so-called repletes or 'honey pots' (hence their common name 'Red Honey Ant' and indeed the genus name *Melophorus*, meaning 'honey carrier'). This method of food storage is also adopted by several other seasonally active ants, e.g., *Cataglyphis* (Schmid-Hempel & Schmid-Hempel 1984) of North Africa, *Camponotus* (Froggatt 1896) of Australia, and *Myrmecocystus* (Snelling 1976) and *Prenolepis* (Tschinkel 1987) of North America (the latter store fat, not sugar).

In recent years, *M. bagoti* has attracted increasing attention for its navigational abilities (e.g., Kohler & Wehner 2005; Narendra et al. 2007, 2008; Sommer et al. 2008; Graham & Cheng 2009a, b; for a review see Cheng et al. 2009), thus making a broader understanding of its behaviour and life history desirable.

Material and Methods

The study site is located 10 km south of Alice Springs, NT, Australia, on the grounds of CSIRO Alice Springs. The area is characterised by an arid climate, with an average annual rainfall of 279.4 mm (Commonwealth of Australia 2009). The soil consists of sandy flood plain alluvium (Northcote et al. 1968), and the vegetation is a mosaic of *Acacia* low open woodland and *Triodia* low open hummock grassland (Northern Territory Government 2004), although much of the latter has been replaced by the invasive Buffel grass *Cenchrus ciliaris*. *M. bagoti* is common in the area, and

their nests occur at a density of ~3/ha, which is much lower than previously reported by Muser et al. (2005) from a different location.

The observation of a nest move was made in December 2008, and colony founding was observed between December 2008 and March 2009. As these incidents were unpredictable, observations could not be made systematically. Due to unusually high rainfall in November 2008 (wettest November on record with 156 mm rain), much of the area was covered by fresh vegetation for most of the summer.

Results and Discussion

Nest move

After a full week of rainy weather, some nests of *M. bagoti* reopened their entrance holes on 21 November 2008. In the following three weeks, 12 of 16 observed nests relocated the position of their entrances several times by 5–191 cm (average: 73 cm). This behaviour is usually displayed much more rarely. Occasionally several entrances were in use at the same time. In preparation for other experiments, the area around one of these nests was cleared of vegetation on 25 November whereby a nest chamber very close to the surface was accidentally opened. In the following days the nest relocated its entrance to this new opening (distance: 47 cm, bearing: 190°), closing the old entrance. On 3 December (partly cloudy, max. temp. 40.9°C) at 17.00 h we noticed that this nest was in the middle of relocating to a new nest site (distance: 17.75 m, 205°). A continuous but sparse moving column of ants, including repletes, was observed between the two nest sites. The column was directed to the new nest in almost a straight line. Although most workers went from the old to the new nest, some were observed going the other way. The width of the column varied from a few cm to about 1 m but always seemed to consist of distinct trails. Most, but not all of the repletes were pulled or pushed out of the old nest opening by workers and proceeded to move to the new nest on their own (see Supplementary Material), where some were dragged into the entrance by workers. Because foragers are usually the only ants that leave a nest, repletes are necessarily unfamiliar with the environment around the nest. They must therefore rely

on other cues to find the direction and location of the new nest. There are three possible explanations. Other workers within the nest could convey the information, they might simply follow other ants on the trail, or they might use a system of chemical (olfactory) marking. Indeed, on several occasions workers were seen dragging the tip of their abdomen across the sandy soil (see Fig. 1 and Supplementary Material), a behaviour which has not been observed in *M. bagoti* or any other solitary foraging desert ant so far. These ants may be laying intermittent odour trails. If this conclusion holds true, it will have important implications for future studies on the navigational strategies of this ant species.

We could distinguish two types of repletes, as previously described by Conway (1992): ones with clear, amber-coloured abdomens and ones with milky white abdomens. The sizes of their inflated abdomens were variable. One dealate queen was also observed, and one winged male, but no eggs, larvae or pupae. The queen was dragged all the way from the old to the new nest (see Supplementary Material). All activity ceased at 17.30 h. Over the next few days we checked for activity sporadically. The old nest was now presumably abandoned. On one occasion some workers and one replete from another nearby nest (distance: 19.98 m) entered the old abandoned nest. However, no further activity was observed at the old nest after this incident. At the new nest excavating activity was at first very high, but during the following days the activity slowed down considerably and eventually came to a stop. The nest reopened on 8 January and remained active until the end of the season.

Although nest emigration behaviour seems to be common in forest-dwelling ant species (Smallwood 1982), this does not seem to be the case for *M. bagoti*. Once a nest is established, its location usually does not change over many years (personal observation). In the described case the move was probably triggered by our disturbance.

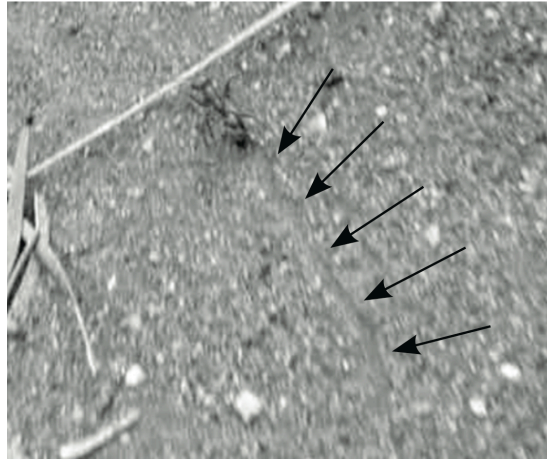


Figure 1: A worker of *M. bagoti* dragging her abdomen across the sandy surface during a nest relocation. Arrows indicate the track left behind in the sand. Still photo taken from a film sequence, credit A. Wystrach.

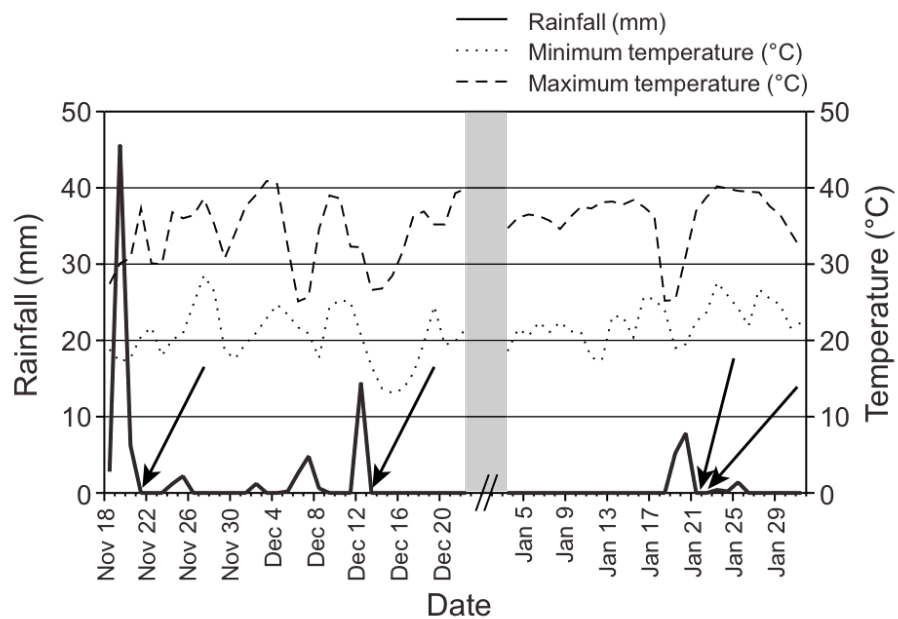


Figure 2: Timing of mating flights in *M. bagoti* during the summer 2008/09. Daily rainfall and temperature (min./max.) are shown for the time period from 18.11.08 to 31.01.09, excluding the period from 23.12.08 to 02.01.09 when no observations were made (indicated by grey bar). Arrows indicate observed mating flights. Climate data from Bureau of Meteorology (2009).

Colony founding

The founding stage of an ant colony is usually characterised by the same sequence of events. The virgin queen leaves the nest in a mating flight and is inseminated by one or several males. She then looks for a new nest site and starts excavating a small nest, where she lays eggs and rears a small brood (Hölldobler & Wilson 1990).

Several nuptial flights were observed during the summer of 2008/09, always after rainy days (see Fig. 2) and always in the mornings. Heavy rain is a common trigger for the timing of mating flights in desert ants (Hölldobler & Wilson 1990). Sometimes queens and males left the nest together to fly off, at other times only queens did so. At about 10.30 h on 21 January 2009, mating flights occurred at four nests simultaneously. As it had rained for the two previous days, it was humid, overcast and warm (61% RH, 29°C at 9.00 h). From this synchronised behaviour, we can surmise that mating occurs in swarms, although no such mating site could be located. One mating was actually observed: an already dealate queen was found on the ground, surrounded by several males, of which one copulated with the queen once for a few seconds.

The following day, a dealate queen was observed leaving a nest at 10.15 h and was followed as she wandered around the area up to a maximum distance of 50 m from the nest entrance, regularly seeking thermal refuge on small plants and twigs. During this time, she copulated once with one male and three times with another male. On both occasions the queen had climbed onto a small plant and remained motionless while the male flew around her. This behaviour is somewhat reminiscent of the sexual calling behaviour of some ponerine ants (Hölldobler & Haskins 1977). The copulations lasted from a few seconds to about half a minute. As all the observed copulations involved dealate queens, they were obviously not regular matings; it seems though that queens readily mate even after they have broken off their wings and possibly even attract males chemically. After 1 h 50 min we stopped following the queen; it is not known if she returned to the nest.

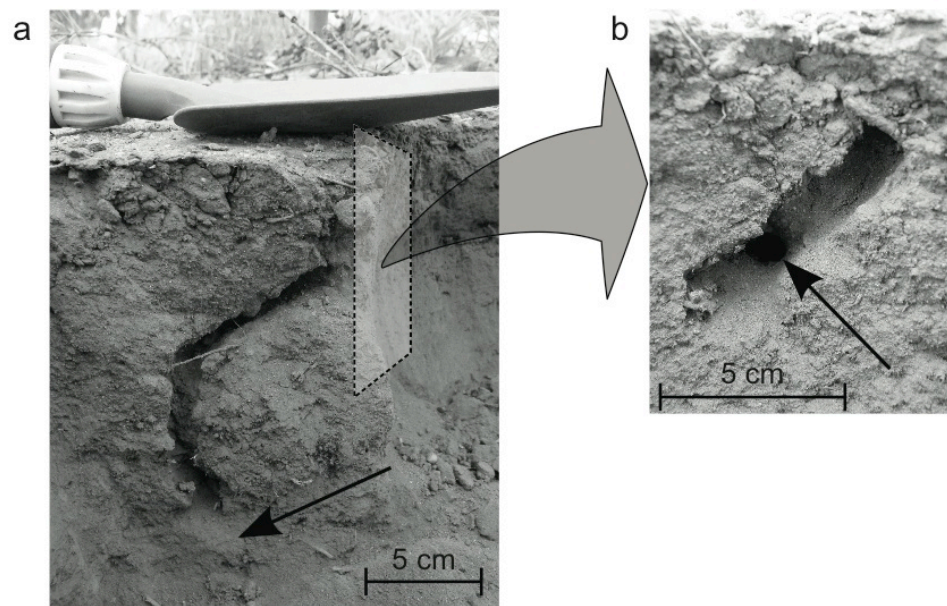


Figure 3: (a) Overview of an excavated founding colony of a *Melophorus bagoti* queen. Arrow indicates the location where the dead queen was found. (b) Close-up of the chamber encountered during excavation, the part of the channel leading to the chamber has been removed. Arrow indicates the channel leaving the chamber on the other side; see text for details. Photo credit P. Schultheiss.

Another dealate queen was seen being followed by a flying insect (probably Diptera, Syrphidae, of which the subfamily Microdontinae has larvae that prey on ants in their nests; the adults are usually found in the vicinity of ant nests; Cheng & Thompson 2008). It followed the exact path the ant took at a constant distance of about 10 cm (see Supplementary Material) until it eventually lost the ant and flew away after searching for a little while.

Queens founded new colonies independently and without the help of other queens or workers (haplometrosis, see Hölldobler & Wilson 1977); this mode of colony founding is common in formicine ants (Hölldobler & Wilson 1990; Keller 1998). However, nothing is known about the number of queens in later colony stages or other populations of *M. bagoti*. For example, in North American ants of the genus *Myrmecocystus*, which can be regarded as the ecological equivalent to *Melophorus* (Andersen 1997), founding queens are often joined by other queens after they have excavated the first nest chamber alone (Bartz & Hölldobler 1982). Also, some desert ants in North America, including *Myrmecocystus*, display considerable geographic variation in their mode of colony founding (Rissing et al. 2000). We observed a total of 21 dealate queens at their attempts to establish new colonies (all on 21 January). Of these, only five were in a completely open place, while the remaining queens chose a spot in the shade of a little plant or twig. Here the queens started to dig at a shallow angle, using their mandibles (see Supplementary Material). They continued digging for sometimes several hours. In one case, the queen had chosen a site that was close to an already existing nest (distance: 7.70 m), and workers from this colony apparently attacked and killed the queen. While several workers dragged the dead queen away, one worker closed the hole of the queen rapidly. After two days, 12 of the 21 holes were closed, rising to 15 after another four days; by 10 March, only one remained open (although obstructed by a branch). All colonies can thus be regarded as failed, for reasons unknown. Four of the closed founding colonies were then excavated. Three of these continued as a narrow channel underground for 2–10 cm, ending in a dead end with no remains of the queen, being wholly or partially filled with debris. The fourth hole started as a narrow channel, slowly sloping downward before opening into a small chamber (length: 7.5 cm). This was oriented at a right angle to the channel but diagonally to the surface, at a depth of 4–9 cm below ground (see Fig. 3b). The channel then continued downwards at roughly 45° for

another 8 cm, turned abruptly downward, and ended without a chamber at a total depth of 16 cm below ground (see Fig. 3a). Remains of a dead queen were found at the end of the channel, and parts of the channel were filled with debris.

The fact that there was no nest chamber at the end of the channel indicates that the queen died before she had fully excavated the founding nest. Although the observations presented here are necessarily incomplete and many important questions remain unanswered, they do offer a fascinating insight into the early stages of an ant colony.

Supplementary Material (video) accompanies this paper and is available online at <http://www.hindawi.com/journals/psyche/2010/435838/sup/>

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CHAPTER III

Finding food: outbound searching behaviour in the Australian desert ant *Melophorus bagoti*



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Finding food: outbound searching behaviour in the Australian desert ant *Melophorus bagoti*

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Abstract

Foragers of *Melophorus bagoti* often return to previously rewarding sites to search for more food items. They are opportunistic scavengers that exploit both protein and carbohydrate food sources. Under natural foraging conditions, protein food items are distributed sparsely and randomly, whereas carbohydrates come in patches that are often renewable. This makes for vastly different foraging scenarios that a single forager is confronted with. In theory, foraging performance can be greatly improved if foragers are able to adjust their strategy to different food item distributions. This could be achieved through individual foraging experience or by employing pre-existing, intrinsic foraging strategies. We investigated this by offering both kinds of food with the same distribution: as a renewable food source at a fixed location. After removal of the food source, outbound foragers displayed an area-restricted search centred on its location. Searches for protein had a greater spread than those for carbohydrates, which matches the natural distribution pattern of these food types. However, searches for both kinds of food follow the same general strategy, which is best described as a Brownian-like walk. We suggest that the observed adaptive behaviour is a result of differential learning effort.

Keywords: Desert ant – foraging – learning – systematic search – random walk – Lévy walk.

Introduction

Foraging ants have to cope with two major difficulties: how to find food and how to find the way back to the nest. Here we focus on how ants search for food items. In nature, food sources can occur at very different densities (sparse or dense) and distributions (patchy or randomly distributed), and food sources can be renewable or depletive (Stephens & Krebs 1986; Bell 1991). Certain types of food, however, have typical distribution patterns. Nectar from flowers, for example, usually comes in patches as one plant often has several flowers, and the food source is generally renewable as the nectar is replenished; the same is true for honeydew excretions from aphids. Dead insects on the other hand are usually randomly distributed as they remain where the insect happened to die, and they are depletive.

Many animals have specialised in the exploitation of food sources whose distribution in space has a typical pattern; it is conceivable that there is considerable selection pressure for search strategies that increase the encounter rate with food and therefore their foraging efficiency (Pyke 1984; Bell 1990; Ydenberg 1998). A large number of studies have focused on identifying optimal search strategies for a diverse array of foraging scenarios, and also on finding evidence of these strategies in the movements of naturally foraging animals (e.g., Hoffmann 1983; Bartumeus et al. 2005; Lomholt et al. 2008; Sims et al. 2008; Scharf et al. 2009; Papastamatiou et al. 2011). They usually concern free-roaming foragers that have no prior knowledge of the distribution of food items. But some animals also return to a location where they have previously found food, as it could offer a continued food supply, for instance a food patch, a large food item, or a renewable food source (e.g., Schmid-Hempel 1984; Crist & MacMahon 1991). They are able to learn the location of this food source, and their foraging behaviour is shaped by experience. If they fail to locate this site, they engage in area-restricted searching behaviour (Pyke 1984; Stephens & Krebs 1986). Their search path is commonly made up of loops that repeatedly bring the animal back to the area where the food is most likely located. Similar selection pressure toward search efficiency can be expected here. Previous work on the ant *Formica schaufussi* has shown that foragers adapt some parameters of their search paths to the type of food previously encountered at that location: carbohydrate food leads to tighter searches of longer duration than protein food

(Traniello et al. 1992; Fourcassié & Traniello 1994). They show this pattern after only one previous visit to the site and it does not change much after repeated offering of the same food type (Fourcassié & Traniello 1993). The authors suggest that the foraging ants have a 'resource-related predisposition' that allows them to adjust their search effort to the different distribution patterns of carbohydrates and proteins in nature. However, the nature of this predisposition remains unclear; it may depend on extrinsic (e.g., learning, perceptual) or intrinsic (e.g., genetic, predetermined) mechanisms (Bell 1990). Fourcassié & Traniello (1994) suggest two possible extrinsic mechanisms. Firstly, search path properties may depend on olfactory stimuli that are used to detect food items. In ants, the detection radius for protein food is greater than for carbohydrate food; a search pattern for protein odours would thus cover a larger area (Pyke 1983). Secondly, the tightness of search may depend on the invested learning effort. A higher learning effort would result in a more precise memory of the food location and thus a tighter search pattern. A possible intrinsic mechanism could be based on predefined, innate search strategies or 'movement rules' that are optimised to find food items with a typical distribution in time and space (like carbohydrates or protein). Encounter of a specific food type could trigger the use of the appropriate strategy in the subsequent search. Advances that have been made in recent years in the field of optimal search theory enable us to investigate the use of different movement strategies.

In theoretical models of searching, the basic movement pattern of a searching animal is generally considered to be made up of segments of straight movement and incidents of reorientation, and to be based on a random walk (Bell 1991). The lengths of the straight segments are drawn at random from probability distributions. Depending on the distribution of food items, models based on certain mathematical distributions can be more successful at locating these items than others. Commonly proposed foraging models are variants of the Brownian walk, based on a Gaussian distribution, and the Lévy walk, which is based on a heavy-tailed (and scale free) power law distribution (Shlesinger & Klafter 1986; Viswanathan et al. 1996, 1999). Although the question of Lévy walks in nature is still being debated (see for example Edwards 2011; James et al. 2011), several empirical studies appear to provide evidence of such movements in animals (Sims et al. 2008; Humphries et al. 2010;

Hays et al. 2012). It has been proposed that Lévy walks could be a widespread searching strategy among central place foragers such as ants and bees (Reynolds et al. 2007a, b; Reynolds & Rhodes 2009). Two recent studies of *Melophorus* ants (Schultheiss & Cheng 2011; P. Schultheiss, A. Wystrach, E. L. G. Legge & K. Cheng, submitted manuscript), however, showed that they do not use a Lévy strategy when searching for their nest entrance.

Our experiments investigate the searching behaviour of *Melophorus bagoti* foragers that are attempting to re-locate a previously experienced, stationary, and non-depleting food source. By offering two different types of food that have very different distribution patterns in nature, we can test if the ants search for these in different manners. We can also investigate if different movement strategies are used in searching for different types of food. Furthermore, these results will add to our as yet limited knowledge about search strategies in central place foragers.

Material and Methods

Study Species and Study Site

Melophorus bagoti is widespread in the semi-arid grassland deserts of inland Australia. Foraging ants are diurnal and highly thermophilic (Christian & Morton 1992) and venture out solitarily to find dead insects, seeds, and sugary plant excretions (Muser et al. 2005; Schultheiss et al. 2010). Due to their special thermal niche they are the only ants that forage during the hot part of the day. They are exceptional navigators and can use both visual navigation and path integration (a mechanism that keeps track of the distances and directions walked) to find their way around (Narendra 2007a, b; Cheng et al. 2009). Foragers repeatedly visit the same foraging areas (Muser et al. 2005), and establish habitual routes between the foraging area and the nest (Kohler & Wehner 2005; Wystrach et al. 2011).

The study site is located ca. 10 km south of Alice Springs and has an average annual precipitation of 287 mm (Australian Bureau of Meteorology, Melbourne). The vegetation is made up of *Triodia* sp. hummock grassland (now largely replaced by

the invasive grass *Cenchrus ciliaris*), interspersed with bushes of *Hakea eyreana*, *Acacia* spp., and occasional large *Eucalyptus* spp. trees. Nests of *M. bagoti* occur at a density of ca. 3 per ha (Schultheiss et al. 2010). Experiments were conducted on one ant colony from December 2009 to February 2010.

Experimental Set-up

Adjacent to the nest entrance, an area of 10 × 10 m was cleared of all vegetation, and a grid of 1 × 1 m squares marked out with tent pegs and string. The nest entrance was enclosed, with an opening providing access to the testing area where a Petri dish feeder (distance: 5 m) was placed at the centre of the test area and provided food *ad libitum*. It contained one of two possible types of food for several weeks at a time: biscuit crumbs ('carbohydrates') or fresh pieces of mealworms ('protein'). Although both food types also contain lipids, and mealworms also contain carbohydrates that will be more accessible when cut up, the main components of the two foods are carbohydrates and protein, respectively. Foragers that discovered the feeder returned to it readily to pick up another food item, thus shuttling back and forth between the feeder and the nest entrance frequently. Ants were marked with a day-specific colour at the feeder, and allowed to continue foraging for a minimum of two days before testing. For a test, the nest entrance was fully enclosed and the feeder removed. (Returning foragers could still enter the enclosure from outside.) When a forager appeared at the nest opening, it was lifted out and set down just outside the enclosure, where it could continue its foraging run. Aided by the grid squares, its foraging path was then recorded on paper for about three minutes, or until the ant left the grid or returned to the nest. This set-up may have resulted in unnatural behaviour of protein-fed foragers, as they rarely encounter renewable protein sources in nature. It does, however, enable us to investigate the mechanisms that shape the behaviour of searching ants.

Data Analysis

All ants that displayed a path of at least 15 m length within the test field were considered as displaying searching behaviour. The searching ants tended to move in rather straight lines and changed direction quite abruptly. Digitisation of the search paths could be limited to these turning positions, which retain most of the information. The starting point of a search was defined as a change in direction of 90° or more, with the turn completed within 0.2 m, and the distance to the next point being at least 0.2 m; for subsequent turning points the critical angle was reduced to 45° . This procedure results in a simplified version of the full search path but retains most of the information, and has been shown to deliver robust results in a previous study (Schultheiss & Cheng 2011). It also breaks down the paths into a series of straight segments of different length, connected by turns of varying angle. The structure of search paths from the two groups of ants ('carbohydrate' and 'protein') was compared in regard to (a) spread, (b) segment length, and (c) turning angle and changes of these parameters within each group were also investigated. Spread was measured as the median or mean distance of the turning points from the original feeder position in the middle of the test area (position 0/0), segment length was defined as the shortest distance between two turning points, and turning angle was defined as deviation from the straight direction. For comparisons between groups, Mauchly's sphericity test was used to test for equality of variances. Where necessary, Greenhouse-Geisser or Huynh-Feldt corrections were applied, leading to fractional degrees of freedom.

A straightness index was calculated for the initial outbound journey that led the ant close to the feeder location. This approach path was defined as starting once the ant entered the test grid and terminating once the ant reached the line through the feeder perpendicular to the feeder-nest line ($y = 0$). The index was computed by dividing the beeline between these positions by the actual length of the path taken by the ant.

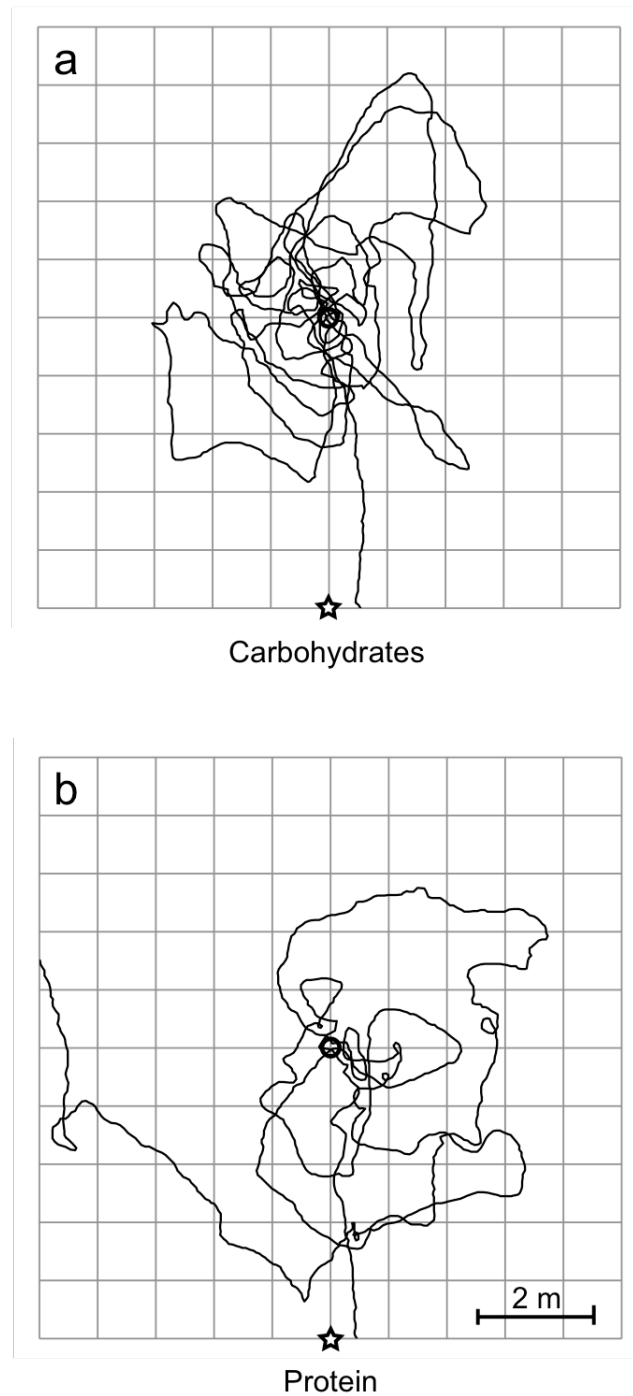


Figure 1: Examples of search paths performed by *Melophorus bagoti* foragers. Ants were trained to a non-depletive food source, which was removed before the test. The open circle marks the previous location of the food source, and the star marks the nest entrance. The ant in (a) had experience of a carbohydrate food source, in (b) of a protein food source.

The movement strategy of searching ants was investigated by calculating frequency distributions of search path segment lengths and finding models that fit the data best. Both exponential and power law models were considered. We followed the procedure laid out in Edwards et al. (2007) and Edwards (2011), which uses the raw, unbinned data to calculate maximum likelihood estimates (MLEs) of model exponents. This method was used to fit models with and without an upper bound to the whole series or the tail end (defined as starting at $a = 2.6$ m), respectively. Bounded models are more realistic when investigating biological systems, as maximum segment length will be limited by physiological or ecological constraints. The upper bound was defined as the maximum value of the distribution. A goodness-of-fit test (G-test with Williams's correction, Sokal & Rohlf 1995) was then performed on the preferred model, to see if it adequately describes the data. In addition, we analysed our data with the method of Sims et al. (2007, 2008), which uses log-binned, normalised (LBN) data. We are aware that this procedure is considered less exact than MLE calculations (Edwards 2008, A. M. Edwards, personal communication). However, performing this kind of analysis here enables the direct comparison with previously published data on the nest searching behaviour of *M. bagoti* (Schultheiss & Cheng 2011). Further information about model fitting procedures can be found in the Supplementary Material.

Results

Structure of Search Paths

Ants that were tested had experience of the unlimited, stationary food source (carbohydrate or protein) for at least two days. During this time they learnt the location of this food source and returned to it frequently. Carbohydrate- and protein-fed ants returned to the feeder with similar frequency. When the feeder was removed, 86% of carbohydrate foragers (total $n = 57$) and 87% of protein foragers (total $n = 60$) returned to the area where it was located and displayed an area-restricted search that was centred on the previous feeder location (Figs. 1 and 2).

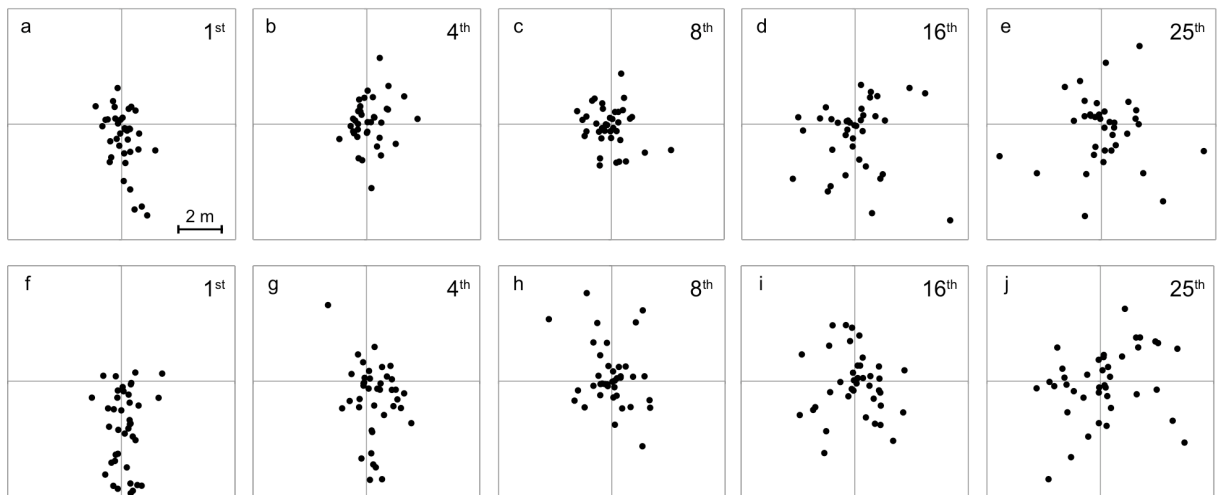


Figure 2: Overview plots showing the positions of turning points as the search unfolds in (a)-(e) carbohydrate and (f)-(j) protein foragers. Single plots from left to right show the positions of the 1st, 4th, 8th, 16th and 25th turning points. In each subplot, the feeder position is located at the centre, marked by the crossing of the grey lines (carbohydrates: $n = 37$, protein: $n = 40$).

The spread of these searches was slightly different between groups: ants trained to a carbohydrate-rich food source displayed tighter searches than ants trained to a protein-rich food source (O'Brien's test for homogeneity of variance: $F_{1,86} = 4.3$, $p < 0.05$; Welch's ANOVA: $F_{1,75.84} = 5.0$, $p < 0.05$; Fig. 3a). It must be noted though that the variance between individual ants was quite large in both groups, and there was also considerable overlap between the two. Figure 3b shows the straightness of the initial approach path from the nest entrance to the feeder position. Foragers in the protein group had significantly lower straightness indices ($t(99) = 2.4$, $p < 0.05$). Looking into the behaviour of ants within each group, further differences become evident. Foragers looking for carbohydrate food started their search close to the feeder (Fig. 2) and then slowly moved outward, away from the feeder location (Fig. 4a). This increase in spread was significant (repeated measures ANOVA: $F_{8,1,299.6} = 4.5$, $p < 0.001$) and followed a significant linear trend ($F_{1,37} = 17.3$, $p < 0.001$). Ants looking for protein food began their search at a greater distance from the feeder ($t(68.5) = -3.7$, $p < 0.001$), quickly moved closer and then stayed at a similar average distance to it (Figs. 2 and 4b). Overall, no significant change in spread was observed (repeated measures ANOVA: $F_{6,1,236.4} = 1.9$, $p = 0.08$). As the search unfolded, ants in both conditions also showed a gradual increase in segment length (Fig. 4c, d; two-way ANOVA: $F_{13.7,1030} = 1.8$, $p < 0.05$, with no differences between groups, $F_{1,75} = 1.2$, $p = 0.29$). The increase followed a significant linear trend ($F_{1,75} = 16.0$, $p < 0.001$). At the same time, no changes were apparent in their turning angles (two-way ANOVA: $F_{22,1650} = 0.7$, $p = 0.8$, and no differences between groups, $F_{1,75} = 1.4$, $p = 0.2$; measured over 25 turning points, ants with fewer turning points being excluded from the analysis; n values as in Figure 4).

Movement Strategy

We then fit models to the segment length distributions to investigate the underlying movement strategy. Within each group, all analyses are based on the same data (derived from $n = 49$ paths for the carbohydrate group, and $n = 53$ paths for the protein group). Figure 5 gives an overview of the distributions. It shows a high frequency of short segments that rapidly drops off as the segment length increases.

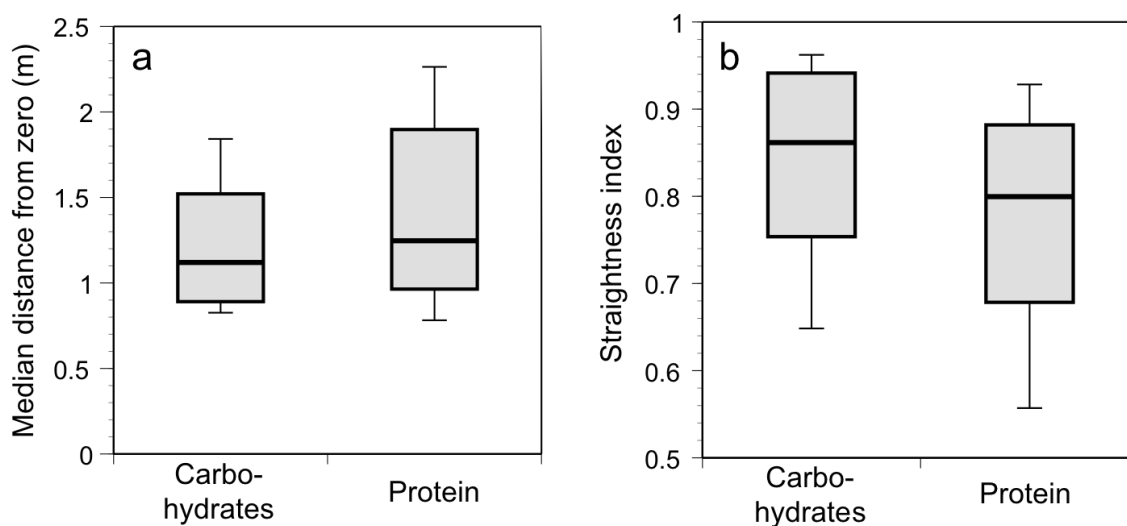


Figure 3: Differences in search path parameters between groups. (a) Search spread of the first 20 m of search path in the two groups (carbohydrates: $n = 43$, protein: $n = 45$). Boxes show medians and upper and lower quartiles; whiskers extend to the upper and lower deciles. Paths with less than 20 m path length were excluded from the analysis. (b) Straightness index of the initial approach path from the nest entrance to the target position. A perfectly straight path will have an index of 1 (carbohydrates: $n = 49$, protein: $n = 52$).

This general pattern, however, is broken by the large values in the second bin, showing segment lengths of 0.4–0.6 m; for carbohydrate foragers, these values are even higher than those in the first bin. This pattern is interesting, but cannot be meaningfully explained by general searching models. For the following model fitting procedures, we therefore only consider segments with a minimum length (x_{\min}) of 0.6 m or larger.

Figure 6 and Table 1 show the results from the analysis following the MLE method (Edwards et al. 2007; Edwards 2011). Results from the analysis following the LBN method (Sims et al. 2007, 2008) can be found in the Supplementary Material (Supplementary Fig. S1 and Supplementary Table S1). The tables include several values that are calculated for model selection. Akaike's Information Criterion (AIC) is used to find the best model in a group (we use the more accurate AICc which includes a correction term); the preferred model has the smallest AIC value. The AIC weight measures the weight of evidence for each model, and the evidence ratio compares the weight of evidence for each model to that of the best one, thus giving a measure of relative likelihood.

The results of the MLE analysis show that, for both conditions, exponential models are strongly preferred over power law models (Table 1). Unbounded exponential models deliver the best results, but bounded exponential models remain viable options in both cases. Goodness-of-fit tests show that the unbounded exponential models describe the data adequately in both groups (G -test: $p = 0.058$ for carbohydrate foragers, $p = 0.230$ for protein foragers). To further investigate possible Lévy walk characteristics, we repeated the analysis with just the tail end of the distribution (Table 1). In both groups, there is no clear preference of one model type over the other, possibly due to the small number of segments that constitute the tail end. But in any case, the estimates for the power law exponent μ are well outside the range of Lévy walks (1 to 3; Viswanathan et al. 1999). The LBN method delivers quite similar results for models fit to the whole series (Supplementary Fig. S1). Although the picture is not quite as clear, a single exponential model describes the distribution adequately in both conditions (Supplementary Table S1).

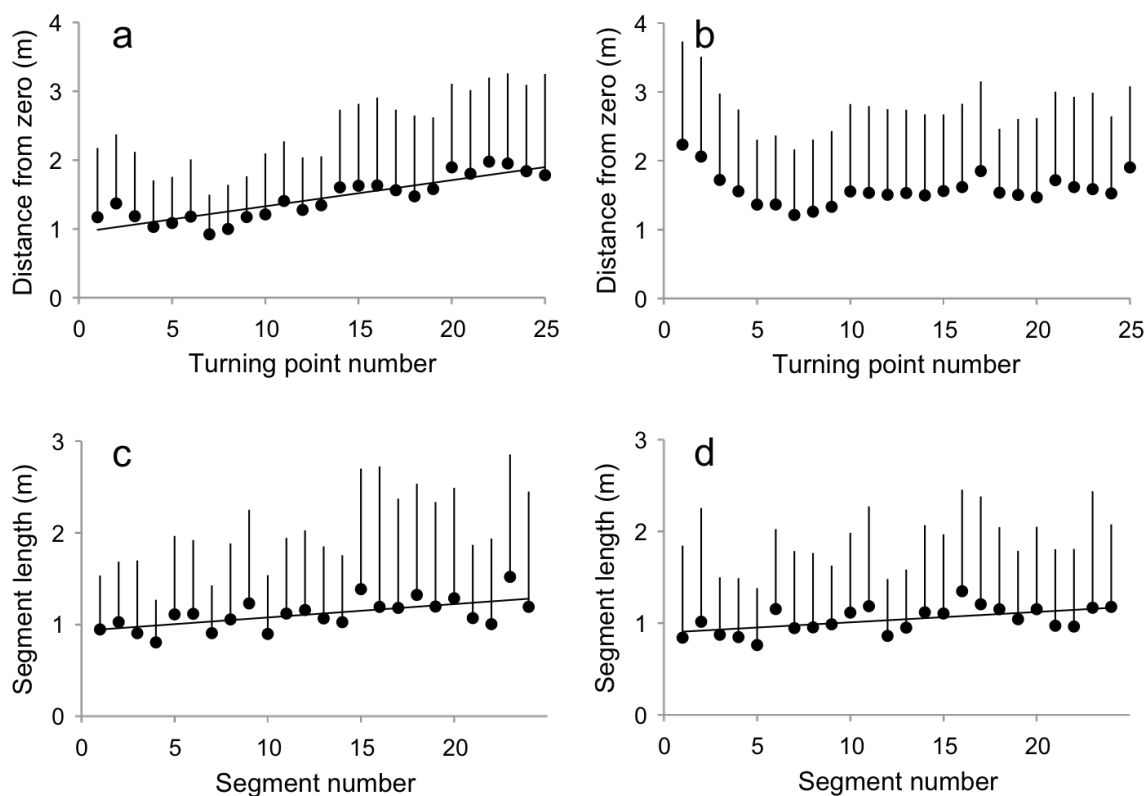


Figure 4: Changes in search path parameters as the search unfolds. Error bars show standard deviation, and black lines show best fitting linear functions. Ants with less than 25 turning points or less than 24 segments were excluded from the analysis (carbohydrate: $n = 37$, protein: $n = 40$). Upper panels show average distance of turning points from zero (the previous feeder location) in (a) carbohydrate foragers and (b) protein foragers. Lower panels show average length of search path segments in (c) carbohydrate and (d) protein foragers.

Table 1: Statistical parameters of curve fitting using the MLE method, for functions fit to the whole series (shown in Figure 6) and to the tail end of the distribution only

	exponent	95% CI	log-likelihood	AICc	AIC weight	evidence ratio
Function fit to whole series						
Carbohydrates						
Exp	$\lambda_{MLE} = 1.047$	0.987–1.109	–1070.874	2145.726	0.514	1
ExpB	$\lambda_{MLE} = 1.040$	0.979–1.103	–1069.908	2145.838	0.486	1.058
PL	$\mu_{MLE} = 2.260$	2.187–2.335	–1180.794	2365.567	$9.402 e^{-49}$	$5.467 e^{47}$
PLB	$\mu_{MLE} = 1.959$	1.868–2.051	–1112.766	2231.553	$1.186 e^{-19}$	$4.334 e^{18}$
Protein						
Exp	$\lambda_{MLE} = 1.100$	1.037–1.166	–1000.513	2005.004	0.663	1
ExpB	$\lambda_{MLE} = 1.097$	1.033–1.164	–1000.168	2006.358	0.337	1.968
PL	$\mu_{MLE} = 2.287$	2.212–2.364	–1122.060	2248.100	$1.081 e^{-53}$	$6.131 e^{52}$
PLB	$\mu_{MLE} = 2.029$	1.937–2.122	–1067.403	2140.828	$2.128 e^{-30}$	$3.117 e^{29}$
Function fit to tail end						
Carbohydrates						
Exp	$\lambda_{MLE} = 0.999$	0.845–1.168	–147.301	298.689	0.373	1.467
ExpB	$\lambda_{MLE} = 0.948$	0.780–1.130	–145.877	297.922	0.548	1
PL	$\mu_{MLE} = 4.347$	3.835–4.917	–153.808	311.704	0.001	982.967
PLB	$\mu_{MLE} = 3.779$	3.150–4.441	–147.823	301.814	0.078	7
Protein						
Exp	$\lambda_{MLE} = 1.102$	0.920–1.307	–112.823	229.744	0.188	2.964
ExpB	$\lambda_{MLE} = 1.083$	0.892–1.293	–112.460	231.119	0.094	5.896
PL	$\mu_{MLE} = 4.740$	4.122–5.435	–112.966	230.030	0.162	3.421
PLB	$\mu_{MLE} = 4.421$	3.711–5.183	–110.686	227.571	0.556	1

Note. Maximum likelihood estimates (MLEs) of function exponents were calculated according to Edwards et al. (2007) and Edwards (2011); the log-likelihood of the estimate is also given. 95% confidence intervals (CI) were obtained with the profile likelihood-ratio test (Hilborn & Mangel 1997). Calculation of AICc, AIC weight and evidence ratio follows Burnham & Anderson (2002). The tail end of the segment length distribution starts at $a = 2.6$ m for both groups (carbohydrates: $n = 147$, protein: $n = 125$). Exp = exponential, ExpB = bounded exponential, PL = power law, PLB = bounded power law.

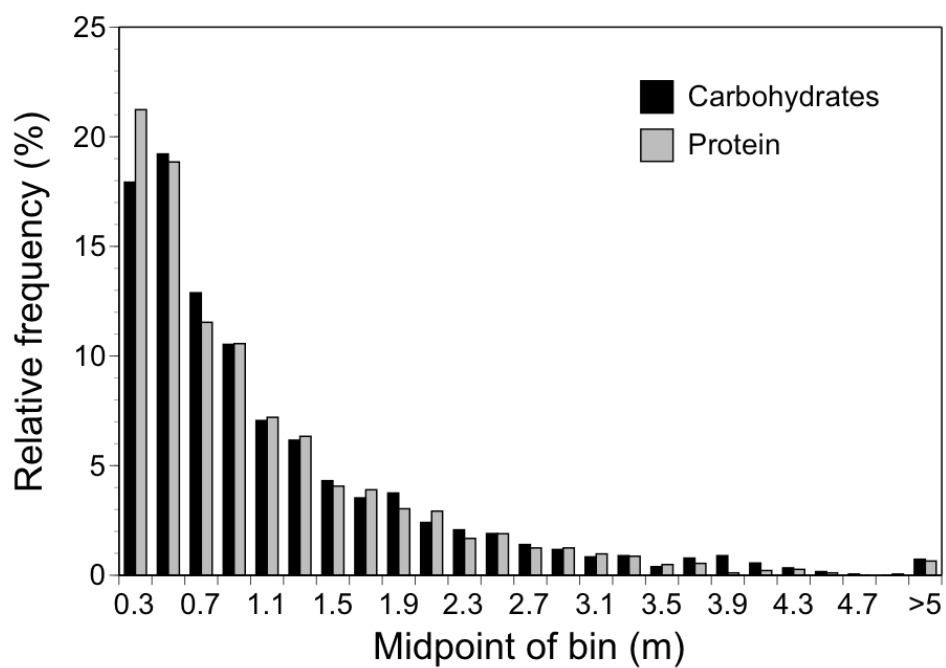


Figure 5: Overview of the segment length distributions from both groups. Data were put in bins of 0.2 m width, starting with the minimum segment length of 0.2 m. Carbohydrate group: $n = 1785$ segments, protein group: $n = 1846$ segments.

Discussion

Foragers of *M. bagoti* make use of both protein and carbohydrate food sources, which have very different distribution patterns in nature. We offered both kinds of food with the same distribution, as a renewable food source, to see if food type alone can trigger different searching behaviour, and if differences are due to the use of divergent search strategies.

In our experiments, *Melophorus* foragers readily learnt the location of a renewable food source (carbohydrate or protein), and displayed a systematic search for it when removed. This search path was centred on the previous food location (Figs. 1 and 2) and was made up of loops of varying size; this looping structure repeatedly brought the ant back close to the target area. Interestingly, the type of food previously available at that location had an effect on the behaviour of ants: their initial approach path to the protein food source was less straight (Fig. 3b), and the spread of searches for protein-rich food was larger than that for carbohydrate-rich food (Fig. 3a). As both food types were offered with the same distribution in space, these differences have to be due to some quality of the food. Several possibilities come to mind as to how these differences are achieved:

(I) The ants could simply be better at learning the location of carbohydrate food than of protein food, and thus be more confident about the location of the food. Carbohydrate resources are typically clumped, so that the chances of another food reward at that site are high. Natural protein, on the other hand, occurs scattered over large areas and is not replenished, so that learning the location of a protein source is usually not beneficial. If learning were 'strategic' or dependent on motivation then carbohydrate foragers might create more accurate spatial memories. Given the costs associated with learning and memory (Dukas 1998, 2008; Hoedjes et al. 2011), it makes functional sense to tailor the amount of learning and the robustness of memory and their associated costs to the expected need for learned information (see also Traniello et al. 1992; Fourcassié & Traniello 1993, 1994).

Better learning in turn should cause a tighter search pattern, in which the spread of the search pattern is based on probabilistic expectations of the reward location. In this view, better learning creates an expected distribution of reward

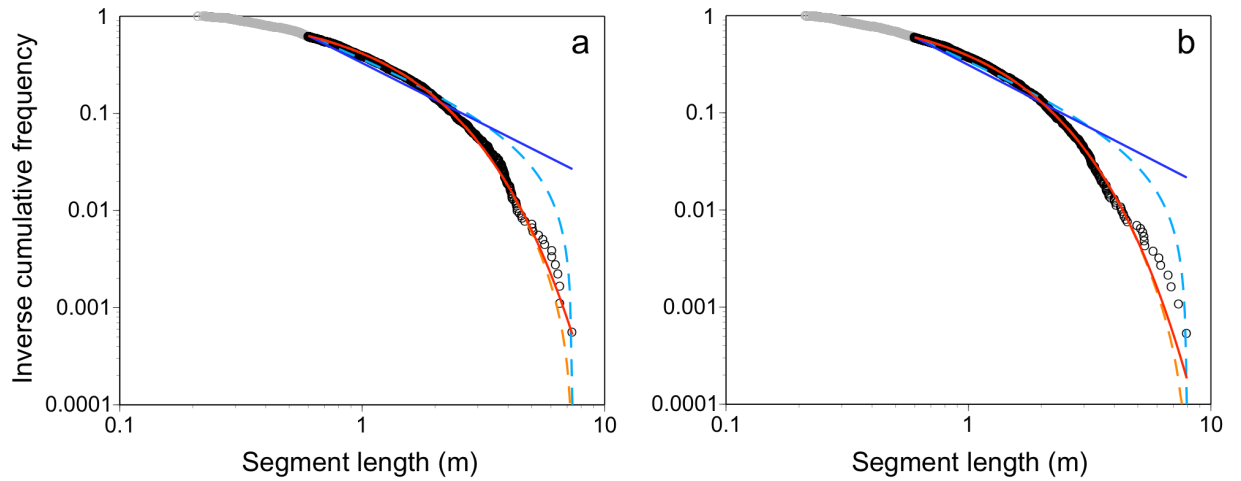


Figure 6: Inverse cumulative frequency distribution plots of segment lengths, for (a) carbohydrate and (b) protein foragers. Note that axes are logarithmic. Values below x_{\min} are shown in grey, and are not considered for function fits. Lines show best fitting functions over the whole series, using the MLE method; red = exponential, orange dashed = bounded exponential, blue = power law, light blue dashed = bounded power law. n values for segments $\geq x_{\min}$: 1122 for carbohydrates, 1106 for protein.

location with less uncertainty (less spread), and search spread is tuned to match these expectations. Ants with a higher degree of uncertainty about a location are known to display larger searches (Merkle et al. 2006), and there is evidence that their path meander increases (Wystrach et al. 2011). The paths of our protein foragers showed both these features (Fig. 3a, b). The stronger meander in the approach paths of protein foragers had further consequences on the search path properties. Carbohydrate foragers moved close to the target position before starting their search, which then slowly expanded outward (Figs. 2 and 4a). Protein foragers, on the other hand, walked to the target in a more tortuous way, to the effect that our search criteria were often met before reaching the target. The approach path was then concluded with the first few search segments before the rest of the path was centred on the target (Fig. 2). In fact, the meandering approach path may already be part of the actual search for protein. Foragers would then appear to ‘switch’ from an intrinsic, forward-drifting search strategy to an extrinsic, learnt-place strategy in the vicinity of the target (Fig. 4b). This behaviour may increase the chances of finding other protein-rich food items on the way to the target, as a tortuous path covers a larger area than a straight path.

The suggestion that ants may be able to learn strategically can be tested experimentally by first training all foragers to a carbohydrate food source; in a second step, one group continues to experience this carbohydrate food source, whereas another group is trained to protein food at the same location (see Fourcassié & Traniello 1993). If learning is strategic, both groups of foragers should then have a similarly accurate memory of the food location, and will search with a similar strategy.

(II) The differences in search spread may be explained by the type of stimulus that is used to locate the food. The foragers may in fact be searching for odour cues that will lead them to the food source. Because the detection radius for protein food is larger than that for carbohydrate food (Pyke 1983), efficient searches for protein odours will cover a larger area. The decrease in straightness of protein foragers’ paths when approaching the reward site (Fig. 3b) could also be interpreted as the behaviour of ants scanning for an odour plume. Odour is known to play a significant part in the navigational toolkit of desert ants and is used in both foraging (Wolf & Wehner 2005) and homing (Steck et al. 2009). Such a hypothesis may be tested by

controlling the odours emanating from the feeder, by sealing the feeder except for letting ants in or by provisioning foods that emit odour but cannot be picked up (e.g., enclosed in a fine mesh).

(III) Foragers looking for the protein food may 'give up' the search faster and move away from that area, thereby increasing their search spread. Unfortunately, 'giving up time' could not be measured directly, as the internal state of the ant is unknown to us: she could well be still moving around in the test area, but not looking for the experimental food source any more. We find, however, no evidence of earlier 'giving up' behaviour (i.e., moving outward, away from the zero position) when looking at the average spread of the unfolding search in that condition (Fig. 4b). If ants looking for protein would indeed move away from the target earlier, we should also see a sharper increase in the segment lengths of their unfolding search paths. This is not the case, as segment length increase was similar in both the conditions (Fig. 4c, d).

(IV) The ants could indeed have different, pre-existing foraging strategies available to them, and use of the appropriate one may be triggered by the food type they previously encountered. If this is the case, we should see some differences in their movement strategies. On the other hand, if the ants do not have different intrinsic strategies to choose from, both groups should display the same movement strategy. This will be shaped by the actual, experienced distribution of food items, which was the same in both conditions.

The movement strategy was investigated by looking at the segment length distributions. In Figure 5, we saw that segments with a length of 0.4–0.6 m occurred more frequently than expected. This may reflect some systematic aspect of their search strategy, for example, an intermittent, small-scale search at the precise feeder location, or may alternatively be due to a systematic sampling error in our methods. In any case, the effect appeared in both groups, and at a similar scale. The remainder of the segment length distribution (≥ 0.6 m in length) was further analysed.

Model fits over the whole series show a very clear preference of exponential over power models in both conditions (Fig. 6 and Table 1). Curve progression is quite smooth in both groups, suggesting that the data are well described by a single function. Adding an upper bound to the exponential model does not further improve

model fits. The calculated slope of the exponential model is very similar in both food conditions (Table 1), evidence that both groups have similar foraging strategies. Results from the LBN method of model fitting are comparable (see Supplementary Material). This supports the idea that, for *Melophorus* foragers, the search strategy is shaped by the actual distribution of food items, and is not derived from some pre-existing foraging strategy (see point IV above). The exponential movement strategy is very similar to the freely roaming Brownian walk, but as the search paths of ants are looping rather than freely roaming, their movements are best described as a 'Brownian-like walk'. Exponential search strategies are also used by *Melophorus* foragers for locating the nest entrance after successful foraging runs (Schultheiss & Cheng 2011; P. Schultheiss, A. Wystrach, E. L. G. Legge & K Cheng, submitted manuscript). This too is a single target, the location of which the ants had previously learnt.

In order to further test for the existence of a heavy-tailed Lévy walk, separate models are also fit to the tail end of the segment length distribution. Here it is not possible to choose between the different types of models, as there is an almost equal amount of evidence for both exponential and power law models (Table 1). Nevertheless, the slope estimates of all power models and their 95% confidence intervals are outside the range of Lévy walks, where $1 < \mu \leq 3$ (Viswanathan et al. 1999). In this, *Melophorus* differs from honeybees, which have been shown to use a Lévy strategy to re-locate a food source (Reynolds et al. 2007b). This difference may, however, be due to differences in experimental procedure: while Reynolds et al. (2007b) tested the bees in an almost featureless open field, our ants were tested in their natural visual surrounding which is cluttered with visual features. It is possible that a systematic search aided by visual navigation and path integration rules out Lévy patterns. Also, the mechanism giving rise to Lévy movements in airborne honeybees may not operate in ants that walk over rough ground.

In conclusion, our study shows that *M. bagoti* foragers search differently for different food types. Although food distribution was identical for both groups, searches for carbohydrates were more concentrated than for protein, and the approach path to carbohydrates was much straighter. This predisposition of behaviour is matched to the natural distribution patterns of food items, as carbohydrate food sources are constant in space and renewable, whereas protein

food sources are not. As all foragers had at least two days of experience of the experimental food source, the differences in searching behaviour are likely to be based on an intrinsic mechanism, and are not due to individually different foraging experience. Our analyses further show that the observed differences between the groups are not a result of the use of different intrinsic movement strategies. Foragers in both groups displayed strategies that are based on exponential distributions, similar to a Brownian walk; there is no evidence for the use of Lévy walks in either group. Although we suggest that differences are due to a decreased learning effort in protein foragers, the details remain to be investigated.

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Supplementary Material

Supplementary Methods

Here we provide a brief overview of the models we applied to our segment length (move-length) data, and the methods used.

Several different procedures have been devised to test for various relationships in animal movement data. A widespread approach is to test if the move-length data follow a mathematical model distribution. Commonly considered model types are exponential models and power law models. Exponential models have the probability density function (pdf)

$$(1) \quad f(x) = \lambda e^{-\lambda(x-a)}, \quad x \geq a$$

and power law models have the pdf

$$(2) \quad f(x) = Cx^{-\mu}, \quad x \geq a$$

where a is the lower bound and C is a normalisation constant which ensures that the integral from the minimum move-length to infinity is 1. C is defined as

$$(3) \quad C = (\mu - 1)a^{\mu-1}$$

Different methods have been developed to calculate or estimate the exponent of these functions (λ for the exponential, μ for the power law model). Especially since the formulation of the so-called Lévy walk the need for an accurate measurement of the exponent has become very important. Lévy walks are power laws where $1 < \mu \leq 3$, and have been proposed to constitute an optimal strategy under certain conditions (Viswanathan et al. 1999). Various simulation studies have been able to point out inaccuracies in some of the methods, but the discussion about which

method should be applied in what context has yet to be fully resolved. James et al. (2011) have recently published an excellent review of Lévy walk models and the different methods for analysing field data.

We applied two different methods of analysis to our move-length data, which we will explain briefly.

Maximum likelihood estimate (MLE) approach

This method uses the raw count data of move-lengths, and is laid out in detail in Edwards et al. (2007) and Edwards (2011). Here we will only provide a summary of the equations that are used.

Any given data set is considered to start at a . If a is set to the lowest value, the whole data set is considered. Alternatively, only the tail end of a set can be considered.

1. Likelihood functions for unbounded models

Here we give the likelihood functions for model distributions that are unbounded and continue on to infinity.

For the exponential model (Equation 1), the log-likelihood function for the unknown parameter λ is

$$(4) \quad \ln[L(\lambda)] = n \ln \lambda + n\lambda a - \lambda \sum_{i=1}^n x_i$$

Solving for the MLE of λ analytically gives

$$(5) \quad \lambda = 1 / \left(\sum_{i=1}^n x_i / n - a \right)$$

For the power law model (Equation 2), the log-likelihood function for the unknown parameter μ is

$$(6) \quad \ln[L(\mu)] = n \ln(\mu - 1) + n(\mu - 1) \ln a - \mu \sum_{i=1}^n \ln x_i$$

Solving for the MLE of μ analytically gives

$$(7) \quad \mu = 1 - n / \left(n \ln a - \sum_{i=1}^n \ln x_i \right)$$

2. Likelihood functions for bounded models

Here we give the likelihood functions for model distributions that have an upper bound b , in addition to the starting point a (see above). The value of b was set to the maximum value of the move-length series.

The pdf for the bounded exponential model is

$$(8) \quad f(x) = A e^{-\lambda x}, \quad x \in [a, b]$$

where

$$(9) \quad A = \frac{\lambda}{e^{-\lambda a} - e^{-\lambda b}}$$

The log-likelihood function for λ is

$$(10) \quad \ln[L(\lambda)] = n \ln \lambda - n \ln(e^{-\lambda a} - e^{-\lambda b}) - \lambda \sum_{i=1}^n x_i$$

The MLE for the unknown parameter λ is analytically intractable, and was subsequently derived by iteration: log-likelihood was calculated with the above equation for incrementally different values of λ in order to find the value that maximises the log-likelihood.

For the bounded power law model ($\mu \neq 1$), the pdf is

$$(11) \quad f(x) = Cx^{-\mu}, \quad x \in [a, b]$$

where the normalisation constant C is given by

$$(12) \quad C = \frac{\mu - 1}{a^{1-\mu} - b^{1-\mu}}$$

For the case where $\mu = 1$, see Edwards (2011), Appendix.

The log-likelihood function for μ ($\mu \neq 1$) is

$$(13) \quad \ln[L(\mu)] = n \ln(\mu - 1) - n \ln(a^{1-\mu} - b^{1-\mu}) - \mu \sum_{i=1}^n \ln x_i$$

The MLE for the unknown parameter μ is again analytically intractable, and an iteration procedure had to be used to estimate μ .

3. Model selection and goodness-of-fit

For both unbounded and bounded models, the AIC for each model can be calculated with

$$(14) \quad AIC = -2 \ln[L(\theta)] + 2K$$

where θ is the exponent (λ or μ). A correction term for small sample sizes was added to the calculated AIC (which then becomes AICc) with

$$(15) \quad AICc = AIC + \frac{2K(K+1)}{n-K-1}$$

where K is the number of free parameters and n is the sample size.

The preferred model (out of the considered models) will have the lowest AICc value. It is not the absolute values of AIC that are important for comparisons between the models, but rather the distances between their AIC values. We therefore calculated AIC differences (Δ_i) with

$$(16) \quad \Delta_i = AIC - AIC_{\min}$$

and further the AIC weight (AICw), which gives the relative likelihood for each model in the set of R models with

$$(17) \quad AICw_i = \frac{e^{-0.5\Delta_i}}{\sum_{r=1}^R e^{-0.5\Delta_r}}$$

and further the evidence ratio for each model compared to the preferred model with

$$(18) \quad evidence\ ratio = \frac{w_1}{w_i}$$

where w_1 is the AICw of the best model. The evidence ratio is helpful in judging the amount of evidence for each given model being the best one.

A benefit of the likelihood approach is that one can compute 95% confidence intervals, using the profile likelihood-ratio test (Hilborn & Mangel 1997), and perform goodness-of-fit tests for the models, using the G-test with Williams's correction

(Sokal & Rohlf 1995). For the G -test, the count data have to be binned. We kept on subdividing the data into bins of equal log size until a bin had a count of < 5 . Expected values were derived by calculating proportional probabilities for the bin ranges from the cumulative distribution function (the integral of the pdf). G was then computed with

$$(19) \quad G = 2 \sum O_i \ln(O_i/E_i)$$

where O_i denotes the observed count value, and E_i denotes the expected value. Williams's correction is calculated with

$$(20) \quad q = 1 + \frac{a^2 - 1}{6nv}$$

where a is the number of bins, n is the sample size, and v is the degrees of freedom. The adjusted G value is then obtained by

$$(21) \quad G_{adj} = \frac{G}{q}$$

and the p -value derived from the Chi-squared distribution.

Logarithmic binning with normalisation (LBN) method

This procedure follows suggestions from Sims et al. (2007, 2008), where further details can be found. It applies a binning procedure to the move-length data. Our data were first put into bins of 0.2 m width. As bins should be of the same log size, we then pooled bins to bring them as close to 0.05 log units as possible. These binned data were plotted on lin/log axes to investigate exponential relationships and on log/log axes to investigate power law relationships. In the first case exponential functions will appear as straight lines, in the latter case power law functions will appear as straight lines. Best fitting models are then derived by a least squares linear

regression on the data points, and the slope of this linear function delivers the exponent of the model (λ or μ). We also investigated double function models by fitting separate linear functions to the short end and the long end of the move-length distribution. The break point between the two functions was derived by iteration, and was placed where the resulting R^2 (of the double function fit) was greatest.

To select the best model, we followed Burnham & Anderson (2002). For each model we calculated Akaike's Information Criterion (AIC) for the least squares case, with

$$(22) \quad AIC = n \ln(\sigma^2) + 2K$$

where

$$(23) \quad \sigma^2 = \frac{\sum \varepsilon_i^2}{n}$$

and ε are the residuals. Note that we are following the method of Sims et al. (2008) here, but that a recent analysis has shown that AIC calculation based on residuals is incorrect in this case (A. M. Edwards, submitted manuscript). AICc, Δ_i , AICw and the evidence ratio can then be calculated as above (equations 15–18).

Supplementary Results

Results of the LBN analysis show a preference of exponential models (Fig. S1a, c) over power models (Fig. S1b, d) in both groups (Table S1). For the carbohydrate foragers, a single exponential model, fit to the whole series (Fig. S1a), best describes the data. The double exponential model, which is fit to the short and long ends of the distribution, respectively, has a slightly better R^2 , but as the breaking point between the two functions adds an extra free parameter, the resulting AIC is higher. For protein foragers the picture is slightly different, as the double exponential model is preferred over the single exponential (Table S1). However, the long end of the distribution is made up of only 7 segments, and appears noisy (Fig. S1c). There is a

strong possibility that the long end of the model is actually fitting noise and not a genuine trend in the data. Overall, we feel there is insufficient support for the double exponential model, and that the data are adequately described by a single exponential model.

Thus, for both carbohydrate and protein foragers, the data are sufficiently well described by single exponential functions. There are small differences between the two conditions, but these are insufficient to conclude a difference in movement strategy. Also, these functions have very similar slopes (Table S1).

Table S1: Statistical parameters of curve fitting in Figure S1. The Akaike Information Criterion with correction term (AICc), AIC weight and evidence ratio were calculated according to Burnham & Anderson (2002). Where the short and long ends of the distribution are fitted separately, the four right columns of the table measure their combined fit

	$f(x)$	R^2	AICc	AIC weight	evidence ratio
Carbohydrates					
Exponential fit of all points	$y = -0.441x + 1.355$	0.971	-66.404	0.719	1
Exponential fit of short end (grey)	$y = -0.477x + 1.430$	0.987	-64.509	0.279	2.578
Exponential fit of long end (black)	$y = -0.972x + 5.143$				
Power fit of all points	$y = -2.789x + 1.116$	0.896	-41.859	$3.366 e^{-6}$	$2.137 e^5$
Power fit of short end (grey)	$y = -1.831x + 0.943$	0.978	-54.595	0.002	366.582
Power fit of long end (black)	$y = -4.357x + 2.050$				
Protein					
Exponential fit of all points	$y = -0.437x + 1.295$	0.962	-59.906	0.035	27.336
Exponential fit of short end (grey)	$y = -0.525x + 1.488$	0.988	-66.523	0.955	1
Exponential fit of long end (black)	$y = -0.340x + 0.817$				
Power fit of all points	$y = -3.038x + 1.137$	0.918	-44.466	$1.551 e^{-5}$	$6.158 e^4$
Power fit of short end (grey)	$y = -1.854x + 0.935$	0.980	-57.344	0.010	98.425
Power fit of long end (black)	$y = -3.707x + 1.470$				

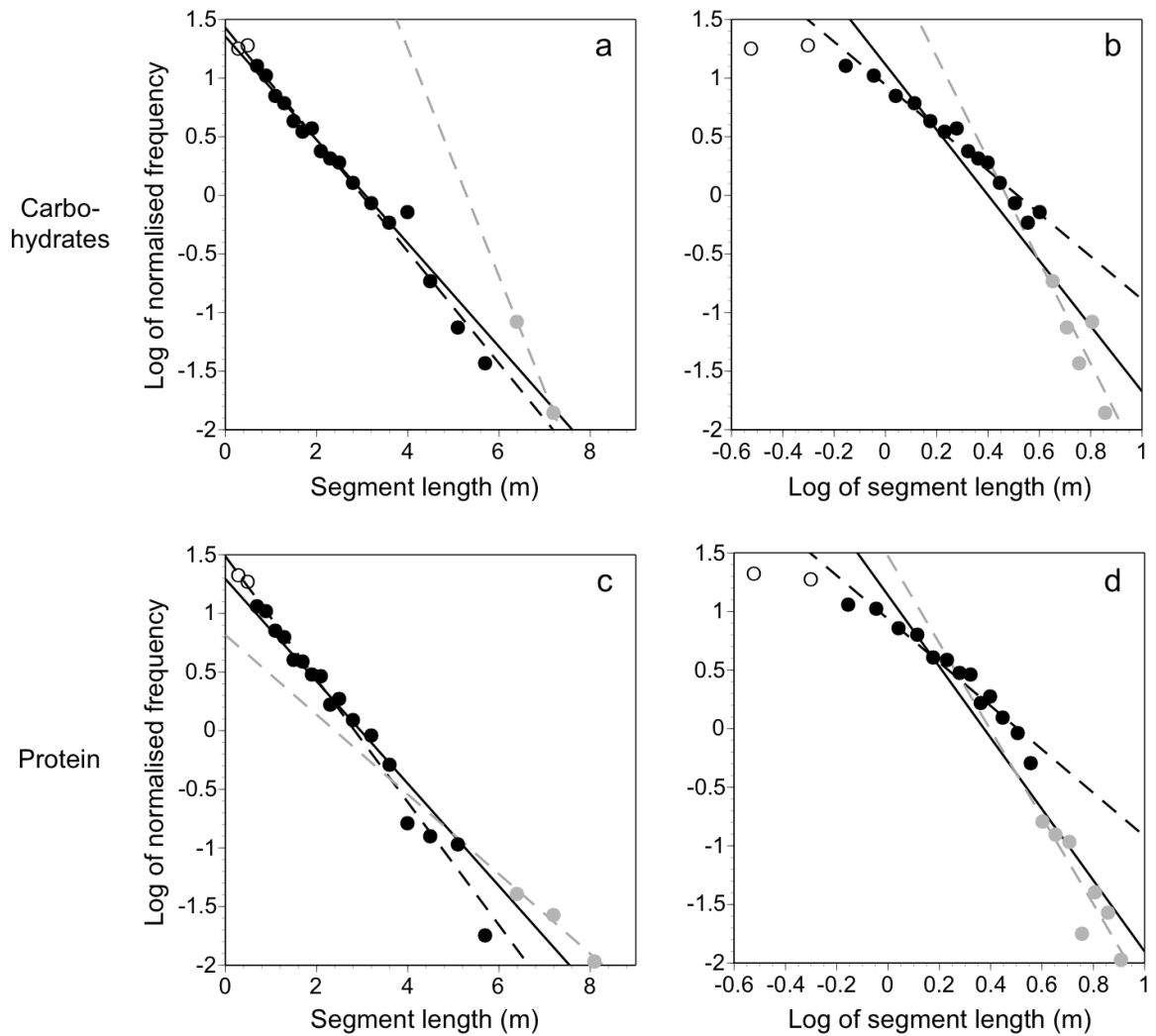


Figure S1: Distribution of segment lengths, following the LBN method, for carbohydrate (a,b) and protein foragers (c,d). Note that the x-axis is linear in panels (a,c) to investigate exponential models, and logarithmic in panels (b,d) to investigate power law models. Black lines show best fitting functions over the whole series, and dashed black and dashed grey lines show best fitting functions over the short end (black dots) and the long end (grey dots) of the distribution, respectively. Open black circles show values below the minimum value ($x_{\min} = 0.6$ m, see main text for details), and were not considered in the function fits. n values for segments $\geq x_{\min}$: 1122 for carbohydrates, 1106 for protein.

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CHAPTER IV

Finding the nest: inbound searching behaviour in the Australian desert ant *Melophorus bagoti*



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Finding the nest: inbound searching behaviour in the Australian desert ant *Melophorus bagoti*

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Abstract

Australian desert ants *Melophorus bagoti* return home after foraging by means of path integration and visual navigation. If these mechanisms do not deliver them exactly at the inconspicuous nest entrance, they engage in a systematic search. Here we describe the structure of this search pattern in detail. Trained ants ran home from a feeder in the natural visual setting where they navigated very accurately, and were then captured for tests on a distant test field after they had almost reached their nest. The search pattern consisted of loops and was centred on the position where the nest was most likely to be located. At first, it covered a rather small area, but then gradually extended outwards to cover a larger area. The search density was also adapted to the preceding outbound foraging distance, with longer distances leading to flatter, wider search distributions. Since the visual surround at the time of capture was similar for ants with all outbound distances, we suggest this is an adaptation to the cumulative error of the homing vector. The frequency distribution of segment lengths in the paths of searching ants does not show characteristics of a Lévy walk strategy. Instead, it is well described by a double exponential model, lending support to a theoretically optimal strategy that consists of a mixture of two random walks, as in the composite Brownian walk strategy.

Keywords: Systematic search – navigation – ants – random walk – Lévy walk – path integration

Introduction

Foraging ants have to cope with two major difficulties: how to find food, and how to find the way back to the nest. Here we focus on how ants locate the nest entrance. Many species of ants use their well-developed chemical (olfactory) sense to follow trails that have been laid out by other foragers of the same colony. These trails lead them away from the nest to foraging areas and also back to the nest (Hölldobler & Wilson 1990). Diurnal desert ants, however, cannot lay elaborate trail systems because of the harsh structure of their habitat: chemical trails simply evaporate too fast on the hot desert floor. Instead, these ants forage solitarily and have therefore developed sophisticated navigational tools to find their way. Like the well-studied ants of the genus *Cataglyphis* (e.g. Wehner & Menzel 1969; Wehner et al. 1996, 2006; Collett et al. 1998; Sommer & Wehner 2004; reviewed in Wehner 2003; Wehner & Srinivasan 2003), the Australian desert ant, *Melophorus bagoti*, uses two main strategies: visual navigation (also termed 'landmark based' or 'geocentric') and path integration ('Euclidean' or 'egocentric' navigation) (Cheng et al. 2009). For visual navigation, of course, visual terrestrial cues have to be present, while path integration, or 'vector navigation' (Wehner 1982), can work in the absence of terrestrial cues; the ants can reach the nest entrance by integrating distances and directions taken during their foraging trip. In *Cataglyphis*, this system has been shown to accumulate errors (Müller & Wehner 1988; Sommer & Wehner 2004; Merkle et al. 2006); in *Melophorus*, Narendra et al. (2007) have shown this accumulation of error for the odometer, which is an integral part of the path integrator. When they divided all individual odometric estimates of foragers by the group mean, variances of groups estimating different distances were similar. In effect, when the foraging distance is increased, the error of the odometric estimate increases proportionally.

Cataglyphis ants in their mainly featureless saltpan environment rely heavily on their path integrator to return home (Wehner 2003; Wehner & Srinivasan 2003). But when *M. bagoti* ants are displaced into an unknown environment, they rely on the homing vector for only about half of the distance to the nest before displaying search behaviour (Narendra 2007). In its natural, cluttered environment, however, *Melophorus* establishes idiosyncratic routes, using visual cues (Kohler & Wehner

2005; Wystrach et al. 2011). If the navigation systems do not deliver the ant exactly at the nest entrance, it engages in a systematic search. Inbound search behaviour can therefore be regarded as a backup system that is employed when other navigational tools are inaccurate or unable to operate. Its structure has been studied in great detail in *Cataglyphis* ants. Wehner & Srinivasan (1981) have shown that it consists of loops of increasing size, and that the path integrator continues to work during the search. Müller & Wehner (1994) have presented a simple search algorithm that is based on principles observed in searching *Cataglyphis*, Merkle et al. (2006) have shown that the spread of the search is adapted to the uncertainty about the nest position, and Merkle & Wehner (2010) have shown that this uncertainty depends on foraging distance, and not actual path length.

Searching behaviour has recently been studied in detail in a number of animals, often with the aim of identifying optimal search strategies. These are commonly based on a random walk strategy that has been ‘specialised’ in a certain way. Two main strategies that have been claimed to be the basis for animal movement are the Brownian walk and the Lévy walk. In both strategies the path is thought to be composed of separate, randomly oriented, linear steps. For a Brownian walk, the length of these steps is drawn from a Gaussian distribution, whereas in a Lévy walk, the length is drawn from a statistical distribution with a power-law tail, making it heavy tailed and scale free (Shlesinger & Klafter 1986; Bartumeus et al. 2005). The Lévy walk can be more efficient than the Brownian walk for foraging animals, albeit in a very specific scenario (searching without prior knowledge for randomly and sparsely distributed, static and nondepleting food resources; Viswanathan et al. 1999). Honeybees, *Apis mellifera*, have been shown to employ a ‘looping’ Lévy strategy when searching for the hive location after displacement (Reynolds et al. 2007a), and it has been predicted to be the optimal strategy for central-place foragers in general (Reynolds et al. 2007a, 2007b; Reynolds 2008b; Reynolds & Rhodes 2009). However, Benhamou’s (2007) simulations show that, in patchy environments, Brownian walks at two different scales, a small-scale area-restricted search (within patches) mixed with large movements (between patches), can be close to optimal. This so-called composite Brownian walk (CBW) closely resembles a Lévy strategy in appearance, and the two may be very hard to distinguish.

For *M. bagoti*, only one study has so far focused on its searching behaviour (Narendra et al. 2008). In the experiments, foraging was confined by one-dimensional channels. In these channels, ants displayed a forward drift in their search patterns; however, it is uncertain if the channel environment had any effect on the search path properties. In this study, we therefore examined the structure of search paths performed by *M. bagoti* ants looking for the nest without constraints, to see whether a forward drifting movement is part of the natural search pattern.

Although similar to *Cataglyphis* in many respects, *Melophorus* is markedly different in others, for example in its ecology and navigational behaviour (see above). By analysing their paths in detail, we investigated to what degree these differences extend into the searching behaviour. We looked into the structure of the search and examined whether their search pattern is adapted to accommodate the accumulated error of the path integrator, as is done by *Cataglyphis* (Merkle et al. 2006). It is also still unclear which search strategy is adopted by *Melophorus* in natural settings. Experiments by Narendra et al. (2008) have shown that, in channels, the distribution of search segment lengths is best described by a mixture of two random walks (RW), as in the CBW strategy laid out by Benhamou (2007), but others have predicted a Lévy search strategy for all central-place foragers. We therefore analysed our data accordingly to identify the underlying strategy.

Material and Methods

Study Species and Study Site

The desert ant *M. bagoti* inhabits the deserts of Central Australia. This ant is highly thermophilic (Christian & Morton 1992) and foragers go out solitarily in the heat of the day to find dead insects, plant exudates and seeds (Muser et al. 2005; Schultheiss et al. 2010).

The field site is located ca. 10 km south of Alice Springs in the Northern Territory, Australia. The area is characterized by a semi-arid climate and has an average annual rainfall of only 279.4 mm (Australian Bureau of Meteorology, Melbourne, Australia). The vegetation is composed of a mixture of *Acacia* sp. low

open woodland with an occasional large *Eucalyptus* sp. tree, and *Triodia* sp. low open hummock grassland, which has been largely replaced by invasive Buffel grass, *Cenchrus ciliaris*.

Experimental Set-up and Data Collection

The searching behaviour of *M. bagoti* foragers from three different nests was recorded from January to March 2009. Foraging ants were trained to a feeder (plastic tub with biscuit crumbs) for a minimum of two days; to this end, ants in the feeder were marked with spots of paint on their thorax and/or abdomen. Feeders were deployed at different distances from the nest entrance (2, 6 and 12 m), but each nest was subjected to only one feeder condition at a time. Individual ants were then captured on their return journey to the nest, just before they entered the nest opening. Tested ants were thus zero-vector ants, which had already run off their calculated vector based on path integration. They were transferred in the dark to a test field of 10 × 10 m, which was cleared of all vegetation and located ca. 70–120 m away from their nest. From this distance, none of the terrestrial cues around the nest entrance were visible, and ants engaged in a systematic search pattern. After release, their search path was recorded for a minimum of 2 min, and a maximum of ca. 5 min (depending on their running speed) or until the ants left the test field.

Recording was facilitated by a grid of 1 × 1 m squares made with tent pegs and string, and a corresponding grid of reduced scale on the data sheet, where the whole search path was recorded. Only ants that still carried a biscuit crumb were tested, and each ant was tested only once. Testing was carried out in the mornings and afternoons, but not during midday when foraging activity usually slows down considerably because of the heat, and only if the cloud cover did not exceed 75%, thus making sure that potential skylight cues were available to the ants (see Wehner & Müller 2006).

Data Analysis

The search paths were then scanned and digitized using GraphClick (Arizona Software, <http://www.arizona-software.ch>). As changes in direction tended to be abrupt, all paths were digitized in regard to turning positions. These points in a path contain the most information. We defined criteria that rigorously describe a turning point: the change in direction had to be at least 45° , the turn had to be completed within a radius of 0.2 m around that point, and the distance to the next turning point had to be at least 0.2 m. These parameters were chosen in regard to the size (ca. 6–12 mm) and running speed (0.22 ± 0.05 m/s) of the ants and the accuracy of the recording technique. Using this procedure, we broke down the search paths into a series of straight segments of different lengths. This data set was then used as the basis for all subsequent analyses. By calculating median or mean values for comparisons between groups, we circumvented problems arising from our digitizing method (varying number of turning points as a result of different segment lengths). It has to be kept in mind though, that in the rare cases where the change in direction occurred gradually, our method may result in a slight undersampling of turns. It also preferentially omits small turning angles and very short segments. By having a subset of the paths digitized by a second person, our method was shown to deliver repeatable results (Pearson $r > 0.99$). Digitizing a subset of paths with a critical turning angle of 60° resulted in very similar data (Pearson $r > 0.99$), adding robustness to the method used. By establishing this digitizing procedure, we were able to use the same data set for both sets of analyses (search path structure and search strategy, see below), thereby enabling us to discuss the interconnections of the two concepts.

To look for drift of the search paths in feeder–nest direction, we rotated paths so that the extended feeder–nest direction pointed in the same direction in all paths. Search patterns of ants in the three conditions (feeder–nest distances of 2, 6 and 12 m) were compared in regard to (1) spread, (2) turning angle and (3) segment length. As a measure of spread we calculated the median distance of the turning points from zero (the release point), similar to methods used by Merkle & Wehner (2009). Turning angle was calculated as deviation from the straight direction, and segment length was measured as the Euclidean distance between two successive



Figure 1: Example of a search path performed by *M. bagoti*. The ant was captured at the nest entrance after returning from a foraging run and released in a distant test field. Black circle at centre denotes the point of release; each grid square is 1 m².

turning points. To compare early parts of the search with later parts, we calculated cumulative path lengths by summing the lengths of separate segments. Paths were then truncated at a total length of 20 m and again at a length of 40 m.

Unless otherwise specified, multiple comparisons between groups were performed using two-way analyses of variance (ANOVA), with Student–Newmans–Keuls post hoc tests for comparisons between single groups.

To investigate the search strategy, we looked at the frequency distribution of segment lengths and calculated best-fitting power and exponential models. Data were put into bins of the same linear size (0.2 m) and, following recommendations by Sims et al. (2007), pooled to make bins of similar log size (as close to 0.05 log units as possible). Data were then normalized according to bin size. As results at each foraging distance were similar, all the data were pooled. In addition, the analysis of segment length distributions was repeated using the unbinned data, following methods proposed by Edwards et al. (2007).

Results

General Search Characteristics

We looked at the searching behaviour of ants in a distant test-field, after they had completed their homebound run in their normal environment. Under no condition did searching ants display any systematic progressive drift in the continued feeder–nest direction (measured as slopes of linear fits on mean displacements along the feeder–nest direction of the first 40 turning points; 2 m: 0.006, $n = 69$ paths; 6 m: 0.023, $n = 82$; 12 m: -0.001 , $n = 93$). Instead, the search was centred on the point of release and consisted of loops of varying sizes, which repeatedly brought the ants back close to the point of release (Fig. 1).

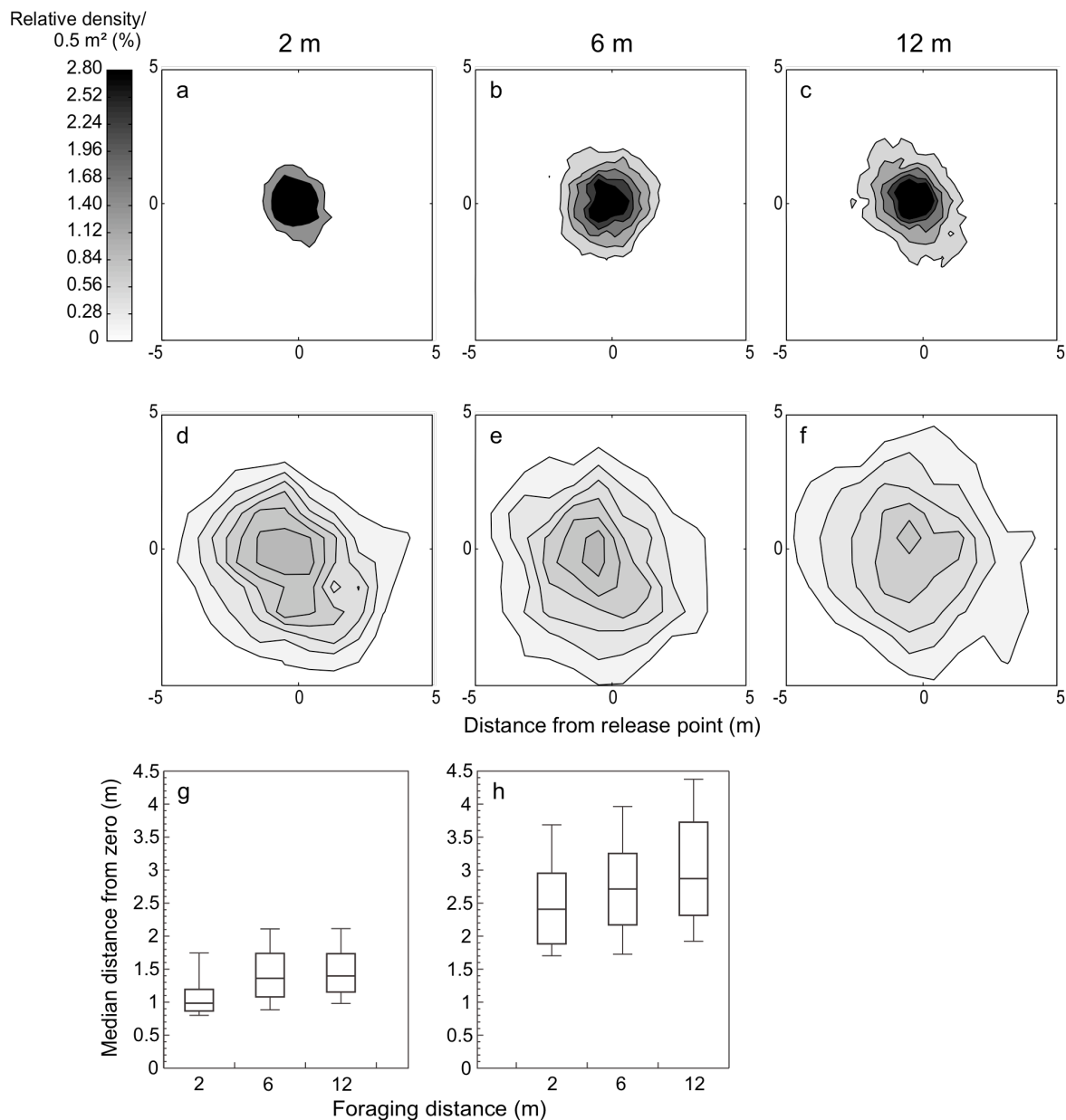


Figure 2: Extension of search patterns in the different conditions. Density plots of (a)–(c) the early part (0–20 m), and (d)–(f) the later part (20–40 m) of search paths in the three conditions: (a) and (d) foraging distance 2 m; (b) and (e) 6 m; (c) and (f) 12 m. (g) Spread of the early part and (h) later part of the search paths. Boxes show median, upper and lower quartiles; whiskers extend to upper and lower deciles. Only paths of 40 m or more in length were considered (2 m: $n = 70$; 6 m: $n = 83$; 12 m: $n = 106$).

Detailed Analysis of Search Behaviour

The length of the preceding foraging run had significant effects on the spread of the search paths, with an increased distance leading to greater spread (main effect of outbound distance: $F_{2,256} = 13.3$, $p < 0.001$; a post hoc test showed significant differences between all groups, $p < 0.05$, except for 6 m versus 12 m; Fig. 2). In all conditions, the search was more concentrated at the beginning (0–20 m of path) than at later stages (20–40 m of path; main effect of stage of search: $F_{1,256} = 603.0$, $p < 0.001$). Figure 2g, h suggests a similar ratio of increase from early to later search at all outbound distances. Computing this ratio at each outbound distance reveals that the three groups were not significantly different on this measure (one-way ANOVA: $F_{2,256} = 2.2$, $p = 0.11$).

Changes in turning angle and segment length as the searches progress are shown in Figure 3. In all three conditions the search began with high mean turning angles, which dropped off considerably as the search continued and eventually levelled out (Fig. 3a–c). The distribution is characterised by both a significant linear trend ($F_{1,9080} = 163.9$, $p < 0.001$) and a significant quadratic trend ($F_{1,9080} = 97.1$, $p < 0.001$). Foraging distance had a significant effect on turning angles ($F_{2,227} = 6.9$, $p < 0.01$, with a post hoc test showing significant differences between all groups, $p < 0.05$, except for 6 m versus 12 m). Mean segment length, on the other hand, increased slightly during search in all three conditions (Fig. 3d–f). Here, too, both a significant linear trend ($F_{1,9080} = 116.2$, $p < 0.001$) and a significant quadratic trend ($F_{1,9080} = 13.9$, $p < 0.001$) are evident. The increase in mean length was slight and did not exceed 0.5 m over 41 segments, but differences between conditions were significant ($F_{2,227} = 18.0$, $p < 0.001$, with a post hoc test showing significant differences between all groups, $p < 0.05$). At the same time, the search gradually extended outward, away from the release point (Fig. 4). Again, analysis shows both significant linear ($F_{1,9080} = 5353.3$, $p < 0.001$) and quadratic trends ($F_{1,9080} = 13.5$, $p < 0.001$), and differences between conditions were significant ($F_{2,227} = 28.9$, $p < 0.001$, with a post hoc test showing significant differences between all groups, $p < 0.05$).

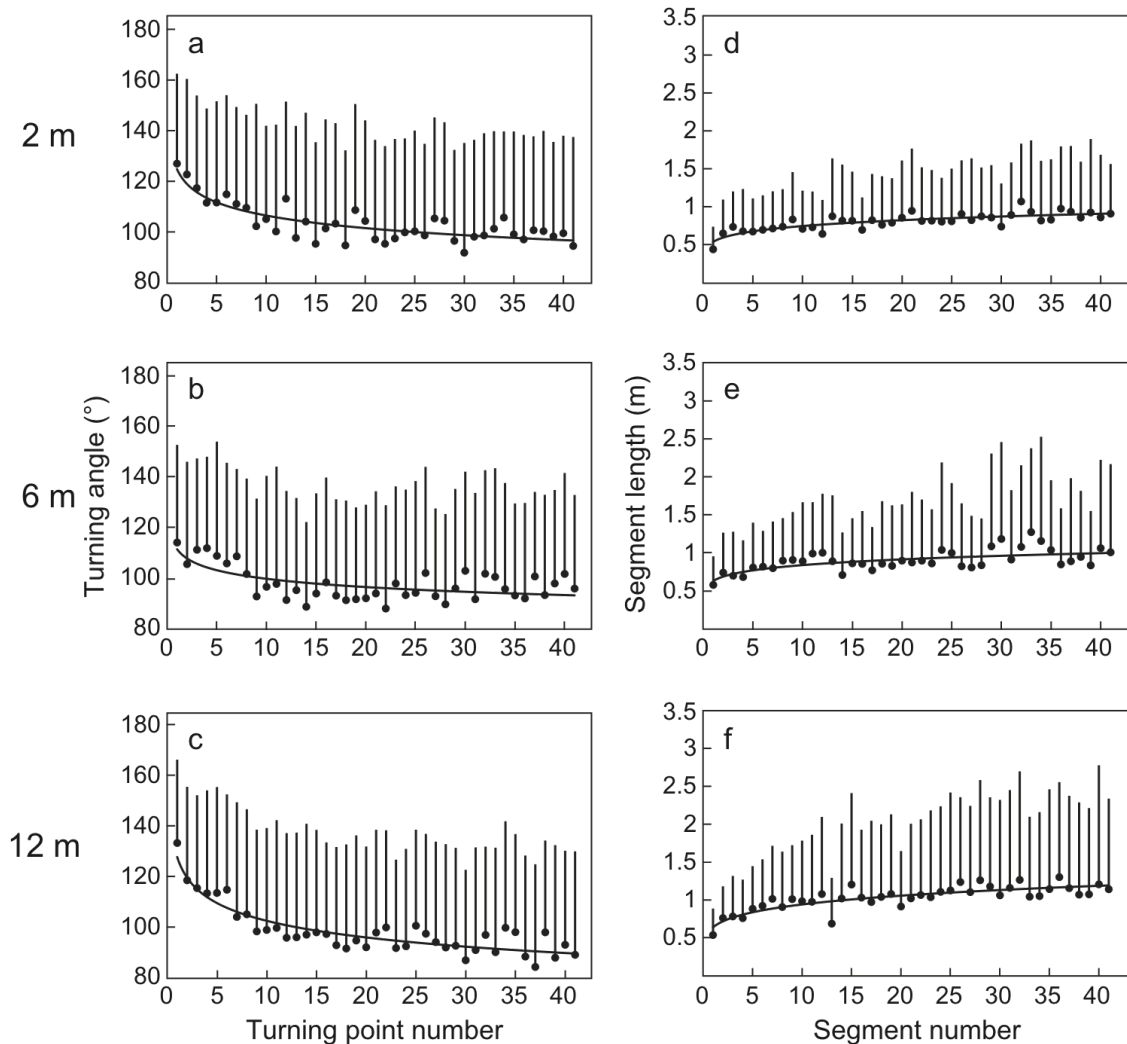


Figure 3: Geometric parameters along the developing search paths. All graphs show the means + SD. (a)–(c) Turning angle along the first 41 turning points between segments. (d)–(f) Segment length along the first 41 segments (minimum segment length 0.2 m). (a) and (d) 2 m condition ($n = 69$); (b) and (e) 6 m condition ($n = 77$); (c) and (f) 12 m condition ($n = 84$). Black lines show best-fitting power functions; ants with less than 41 segments were excluded from the analysis.

Underlying Search Strategy

To find out whether paths of searching ants tended to follow an optimal strategy, and what this strategy might be, we looked at the frequency distribution of segment lengths (Fig. 5). All paths of all conditions were combined ($n = 285$ paths). The same data series is shown in Fig. 5a, b, but the x-axis is logarithmic in Fig. 5a to examine the power-law functions, and linear in Fig. 5b to examine the exponential functions. These data transformations mean that, in each case, the resulting function should be linear. Statistical data of the function fittings are collected in Table 1. This includes the Akaike information criterion (AIC), which is a measure calculated for model selection. For both power and exponential function fittings, the data are rather poorly described by a single function. The distribution is much better described by fitting two separate functions to the short and long range of the distribution. The division of the data into these two groups was made at the point where the r^2 of the resulting double function fit was highest (amounting to an extra free parameter in the models). The fit and the AIC value of the double exponential function are slightly better than that of a double power function (Table 1).

Table 1: Parameters of curve fittings in Fig. 5

	$f(x)$	r^2	$M \text{ error}^2$	AIC
Power fit of all points (dashed)	$y = -2.312x + 0.817$	0.947	0.048	-25.140
Power fit of short end (grey)	$y = -1.359x + 0.828$	0.994	0.006	-42.563
Power fit of long end (black)	$y = -3.148x + 1.371$			
Exponential fit of all points (dashed)	$y = -0.332x + 1.084$	0.950	0.045	-25.656
Exponential fit of short end (grey)	$y = -0.593x + 1.523$	0.994	0.005	-44.009
Exponential fit of long end (black)	$y = -0.246x + 0.511$			

Note. The Akaike Information Criterion (AIC) was calculated according to Burnham & Anderson (2002) and is based on the residual error and the number of free parameters in the model; the lower the value the better. $AIC = n \log(\text{error}) + 2(r + 2)$, with n = number of data points, r = number of free parameters, and $\text{error} = M \text{ error}^2 (n - r - 1)/n$. When the short and long ends of the distribution are separately fitted, the three columns on the right measure their combined fit.

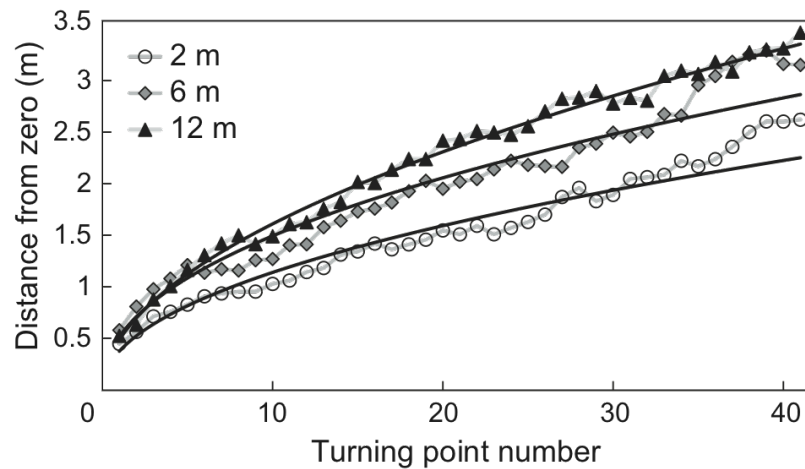


Figure 4: Mean distance of the turning points from the release point (zero) as the search progresses. Values of the first 41 turning points in all three conditions are shown, with the same n values as in Fig. 3. Black lines show best-fitting power functions.

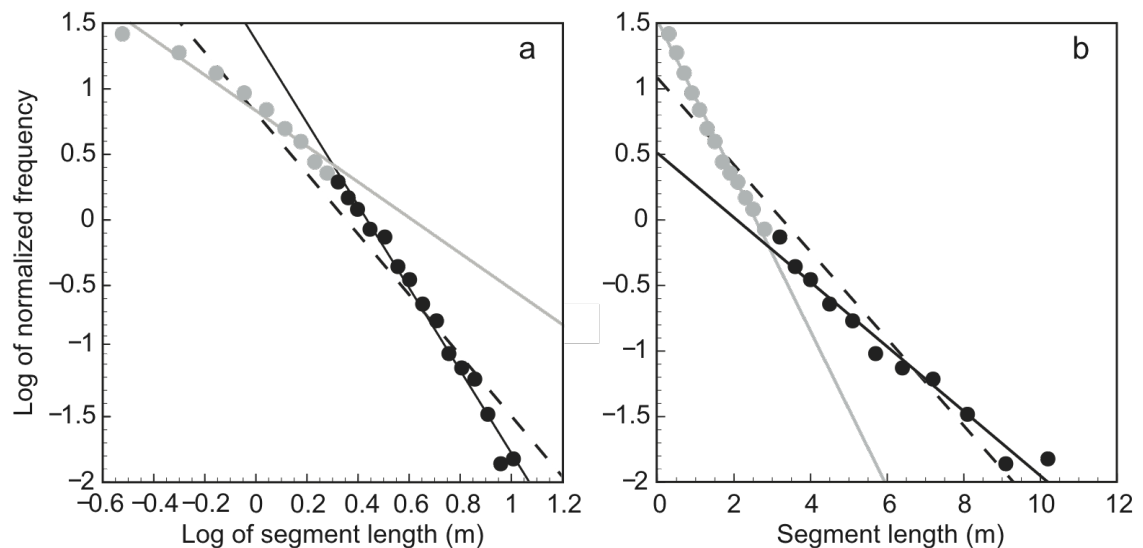


Figure 5: Distribution of segment lengths from all paths combined (n of ants: 285, n of segments: 18 885). (a) Fit of power functions to the data, (b) fit of exponential functions. Dashed lines show the best fit of single linear functions to the whole data set; grey lines and black lines show best linear fits to the short end (grey circles) and the long end (black circles) of the distribution, respectively. Best-fitting functions are summarized in Table 1.

For the tail end of the distribution ($a = 3$), we also tested for power-law and exponential distributions using likelihood, following methods outlined by Edwards et al. (2007). The results are summarised in Table 2. Here too, the exponential model is preferred over the power model.

Table 2: Maximum likelihood estimates (MLE) of exponents for the tail of the segment length distribution

	exponent	95% CI	log likelihood	AIC
Power fit	$\mu_{MLE} = 3.769$	3.603–3.943	–1465.583	2935.166
Exponential fit	$\lambda_{MLE} = 0.658$	0.618–0.699	–1442.795	2889.590

Note. MLEs, 95% confidence intervals (CI), log likelihoods and the Akaike information criterion (AIC) were calculated according to Edwards et al. (2007, p. 1046), using the unbinned data of the tail end of the distribution (starting at $a = 3$).

Discussion

The general structure of the search pattern can be described as follows: across conditions, the search was at first confined to an area close to the point of origin (Fig. 2a–c), with high turning angles and relatively short segment lengths. As the search progressed and gradually extended outward (Figs. 2d–f, 4), the turning angles became markedly smaller (Fig. 3a–c) and the path segments slowly became longer (Fig. 3d–f).

The search pattern of *M. bagoti* is clearly not rigorously fixed, but rather adaptable, as the comparison of spread in the different conditions shows (Fig. 2). A longer foraging distance resulted in a greater spread of the subsequent search pattern. It is worth noting that a post hoc test failed to show significant differences between foraging distances of 6 and 12 m (see Results). The same pattern holds true for the data on turning angles. This may be connected to the fact that an increase from 2 m to 6 m foraging distance is in essence a three-fold increase, whereas an increase from 6 m to 12 m doubles the distance. Over the whole data series, however, the increase in search spread with increasing foraging distance is highly significant. This greater spread is partly achieved through increased segment lengths (Fig. 3).

We suggest that *Melophorus* adjusts its spread of search according to the accuracy of its navigation systems. As we know from the study of Narendra et al. (2007), the error of odometric estimates scales with foraging distance in *Melophorus*. After a longer inbound run, the ants will be less certain about the position of the nest entrance. Increasing the spread of the subsequent search pattern will diffuse the search and distribute it over a larger target area. Similar flexibility has been shown in the search patterns of North African desert ants *Cataglyphis fortis*, which adapt the spread and peak of their search patterns to the length of their foraging distance (see Fig. 3.35 in Wehner 1992). This adjustment has been linked to the uncertainty of the homebound vector (Merkle et al. 2006; Merkle & Wehner 2009). The reliability of the vector decreases with longer foraging distances, and *C. fortis* compensates by broadening its search pattern (Merkle & Wehner 2010).

The observed effect on search paths performed by *Melophorus* in the test field was still very pronounced, although the full inbound journey was performed in the trained visual environment. As the presence of multiple prominent landmarks on the homebound trip should have served to reduce the inaccuracy of navigation (Kohler & Wehner 2005), the remaining uncertainty must be connected to the path integrator. After all, the visual scene at the time of capture for ants with all outbound distances was about the same; all ants were captured near the nest before a test. Results from Merkle & Wehner (2009) with *Cataglyphis* even suggest that experiencing the visual cues close to the nest leads to much tighter searches. In that study, however, all foragers were trained to the same foraging distance; it remains unclear, at least for *Cataglyphis*, whether the experience of nest cues reduces the navigational uncertainty to the same level in all foragers, or whether distance-dependent errors remain. In our findings, the modulation of search patterns on a test field with outbound distance suggests that the errors of the path integration system are not eliminated by the process of visual navigation, or by experiencing the visual cues close to the nest. This is consistent with findings in *C. fortis* that the path integration system is not 'reset' until the ant enters the nest (Knaden & Wehner 2006). We therefore suggest that it is this reduced reliability of the path integrator with increasing outbound distance to which the ants adapt the density and spread of search.

Previous work (Narendra et al. 2008) has examined the search strategies of *M. bagoti* that were looking for the nest entrance in constraining linear channels, and found a systematic drift in the extended feeder–nest direction. We have shown here that they do not display this drift when the search is performed in a natural setting without constraints. Forward drift is therefore not a stereotypical part of the search strategy. By constraining the search to linear channels, the ants may well be learning a motor routine (Narendra et al. 2007), to the effect that they are actually searching for the nest entrance at the end of the channel, and not at a particular location (Narendra et al. 2008). Alternatively, it may be related to the unusual path integration system of *M. bagoti*, in which ants on a distant test field run only half-way home (Narendra 2007). After that, the remaining homing vector may serve to push the search to continue in the feeder–nest direction.

Reynolds et al. (2007a) have recently shown that displaced inbound honeybees engage in searches whose general structure is very similar to the one described here, but they concluded that the underlying strategy is a Lévy-loop searching strategy (Reynolds 2008b). Our results suggest that the intrinsic search strategy of displaced *Melophorus* foragers does not have Lévy-like characteristics (see Tables 1, 2). A single power function does not fit the data very well. The double power function describes the data much better, but delivers a slope for the long end of the distribution that is too steep ($\mu > 3$, with $-\mu$ being the exponent of the power function) to be considered as a Lévy walk (where $1 < \mu \leq 3$; Viswanathan et al. 1999); the estimate of μ using likelihood also lies well outside that range (Table 2). Instead, the good fits and low AIC values for the double exponential model provide evidence that the ants may apply a strategy consisting of a mixture of two RWs. Such a strategy consists of two Brownian search strategies with different mean segment length distributions and, in effect, shows two different search distributions overlaid. The search with the shorter mean length may be employed close to the release point (the fictive nest entrance), while the search with the longer mean length may serve to displace the ant further away from this point into potentially new territory. There was, however, no discernible ‘switching’ between the two RWs in single search paths, as long segments (> 3 m) generally did not appear in clusters. They were performed randomly during search, but tended to become more frequent as the search

progressed. Our interpretation of the strategy as a mixture of RWs is consistent with inbound search data obtained from *Melophorus* foragers running in channels, where a similar combination of two exponential functions fits the data well (Narendra et al. 2008).

As the test field is devoid of familiar cues that could trigger a transition from one search mode to another, this observed mixture of RWs should be considered an intrinsic quality of searching in *Melophorus* ants. Of course, we know nothing about the underlying physiological mechanisms that could generate this pattern. On a theoretical basis, Wehner & Srinivasan (1981) have suggested that desert ants may base their search pattern on probabilistic calculations. The beginning of a search could be based on an *a priori* probability density function for the location of the nest entrance that peaks at the release point, thereby restricting the search to this area. The probability then decreases with the amount of time spent searching that area (*a posteriori* density function), causing an outward shift in the search pattern. After some time, the probability then decreases in that area, and so on. Keeping track of the constantly changing *a posteriori* probabilities will then lead to dynamic searches like those actually observed in desert ants (Wehner & Srinivasan 1981). How the ant's brain might be calculating such probabilities, if at all, remains unclear.

The mixture of two RWs is similar in appearance to the CBW of Benhamou (2007), although, unlike the CBW, it emerges as an intrinsic quality of searching *Melophorus* ants. Reynolds (2008a) interpreted the CBW as a variant of the Lévy walk. The intrapatch Brownian search with short mean segment lengths supposedly corresponds to a Lévy walk with $\mu = 3$, whereas the interpatch Brownian search with long mean segment lengths corresponds to a Lévy walk with $\mu \rightarrow 1$. This refitting of Brownian Walks into the Lévy walk, however, cannot account for either our results or those obtained by Narendra et al. (2008). In both cases, the slopes are decidedly out of line with Reynolds' (2008a) interpretation. In both cases, the short ends of the double power fits have small slopes near -1 , while the long ends of the double power fits have slopes < -3 (see Table 1 here and Table 1 in Narendra et al. 2008). The slopes are, if anything, the 'wrong way around'.

So why do honeybees and desert ants use different search strategies, although their foraging strategy and orientation mechanisms are remarkably similar in many ways? There are some differences in the experimental set-ups that need to be discussed. Reynolds et al. (2007a) described that, after the bees had searched for a while without success around the area where the target was most likely to be located, they refrained from frequently returning to this area and instead adopted a freely roaming search strategy with Lévy properties. This strategy makes sense insofar as it is advantageous to leave this area when an extended search could not locate the target, because the likelihood of the target being located there then actually decreases. This should also be the case for our ants. Their searching behaviour, however, repeatedly brought the ant back to the release point, even after about 10 m. When ants did leave the experimental grid, it was because their search loops had become very large, and not because they adopted a free-roaming search. The fact remains, however, that *Melophorus* utilizes a different search strategy to that of honeybees for nest-centred searches. Another difference between the two experimental set-ups is that Reynolds et al. (2007a) trained and tested their bees in a wide open field; our ants, on the other hand, were both trained and tested in cluttered environments. On our test field, the ants therefore experienced a panorama with a huge visual mismatch that gave them no clue as to where the nest might be. The only available information as to the location of the nest was therefore the release point, whose calculated location was based on path integration. In a wide open field, where the visual panorama is much the same wherever one is, the bees may indeed have ‘exhausted’ the release point after some searching, and adopted a free-roaming search flight, which led them through new terrain with no apparent visual mismatch. These differences in habitat structure could indeed be responsible for the differences observed in the search strategy. If both bees and ants are trying to locate familiar landmarks rather than the actual hive/nest entrance itself, they are trying to locate targets with very different densities. As the Lévy strategy has been shown to be optimal for locating sparsely distributed targets, this may be the appropriate strategy for searching bees in an open field. *Melophorus*, on the other hand, could be looking for rather cluttered, even clustered, cues, and a mixture of two RWs may be the best strategy to do so.

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CHAPTER V

Information content of visual scenes influences systematic search of desert ants



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Information content of visual scenes influences systematic search of desert ants

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Abstract

Many animals – including insects – navigate visually through their environment. Solitary foraging desert ants are known to acquire visual information from the surrounding panorama and use it to navigate along habitual routes or to pinpoint a goal like the nest. Returning foragers that fail to find the nest entrance engage in searching behaviour, during which they continue to use vision. The characteristics of searching behaviour have typically been investigated in unfamiliar environments. Here we investigated in detail the nest searching behaviour of *Melophorus bagoti* foragers within the familiar visual environment of their nest. First, by relating search behaviour to the information content of panoramic (360°) images, we found that searches were more accurate in visually cluttered environments. Second, as observed in unfamiliar visual surrounds, searches were dynamic and gradually expanded with time, showing that nest-pinpointing is not rigidly controlled by vision. Third, contrary to searches displayed in unfamiliar environments, searches observed here could be modelled as a single exponential search strategy, which is similar to a Brownian walk, and there was no evidence of a Lévy walk. Overall, our results revealed that searching behaviour is remarkably flexible and varies according to the relevance of information provided by the surrounding visual scenery.

Keywords: Navigation – systematic search – desert ant – *Melophorus bagoti* – random walk – Lévy walk

Introduction

Many insects use visual objects such as landmarks to navigate through their environment and to pinpoint goals they have previously visited (Cartwright & Collett 1983; Collett 1992; Durier et al. 2003). Natural environments often contain many different landmarks that can be used together for navigation. As one moves around an environment, the visual perception of it will change. For example, objects will appear larger when they are close, and smaller when they are distant. They also may appear to change shape as the observer's perspective changes, and their apparent size and position are constantly modified with displacement. In visually rich environments each location is thus unambiguously characterised by a unique arrangement of visual landmarks.

Central-place foraging insects like bees, wasps, and ants are able to use this visual information to navigate along habitual routes and pinpoint a goal with astonishing accuracy (Wehner & R ber 1979; Collett et al. 2003; Wehner 2003; Cheng et al. 2009; Wystrach et al. 2011a). Since the seminal works of Wehner & R ber (1979) and Cartwright & Collett (1983) there has been much research into how insects acquire and process visual information to find their nest. In complex visual environments, ants do not rely solely on individual landmarks (Wystrach et al. 2011c), but are also guided by cues that are widespread on their panoramic visual field (Graham & Cheng 2009; Wehner & M ller 2010; Reid et al. 2011; Wystrach et al. 2011c). Panoramic visual input at low resolution provides sufficiently accurate information for navigation and is particularly appropriate to deal with the complex depths of natural environments (Zeil et al. 2003; Philippides et al. 2011). Exactly how visual memories are encoded, which features are used, and how information is processed is the topic of a great deal of ongoing research.

Visual navigation is of special importance when insect foragers are locating the nest entrance, which is often inconspicuous when viewed from the surrounding environment. Foragers of flying insects display a specialised behaviour, the orientation flight, when first leaving the nest. They move around the nest entrance in a highly structured manner (in bees: Capaldi et al. 2000; in wasps: Zeil 1993) and often look back towards it (Lehrer 1991). These movements seem to be arranged in

a way that enables them to acquire and memorise visual information that will serve them to find the nest on their return (Zeil et al. 1996). Ants also seem to acquire the necessary visual information when looking back in the direction of the goal: either the nest (Graham & Collett 2006; Müller & Wehner 2010) or a food site (Nicholson et al. 1999).

If the nest is not located, ant foragers engage in searching behaviour, during which they continue to rely on vision if familiar cues are available (Wehner & Räber 1979; Durier et al. 2003; Narendra et al. 2007). However, the characteristics of searching behaviour have typically been investigated in an unfamiliar location where the foragers have never been, to avoid any influence of visual information on the search. From these studies, we know that ant foragers' searches are made up of a series of systematic loops that gradually increase in size while pointing in different azimuthal directions. These loops repeatedly bring the forager back to the starting point of the search (Wehner & Srinivasan 1981; Müller & Wehner 1994; Schultheiss & Cheng 2011). By using this strategy, the searching forager covers an area around the goal, while the goal location itself is visited most frequently; this search distribution matches the probability distribution of finding the goal in that area (Wehner & Srinivasan 1981). We also know that searching ants' movements, i.e. the frequency distribution of path segment lengths, follow a non-uniform pattern which is well described by a double exponential model (Narendra et al. 2008; Schultheiss & Cheng 2011). These search characteristics have been suggested to optimise the search for the nest entrance or familiar landmark cues, but whether they are also displayed within the familiar visual environment of the nest is unknown.

Here, we addressed two questions that arise from the insect navigation literature. First, is the accuracy of searching ants increased in visually cluttered environments? As a cluttered visual scene should contain more navigationally relevant information than a scene with few visual features, it may enable an insect forager to 'compute' positions with increased accuracy. We investigated this by creating two different visual conditions: a natural, relatively open environment, and a visually cluttered environment where several landmarks were added. We then compared the behaviours of ants that are searching for the nest in these conditions. Second, are the systematic search strategies that are performed in unfamiliar visual

environments (see above) also displayed in the familiar surround of the nest? Visual navigation by familiar cues may indeed dominate the search behaviour and inhibit the emergence of other systematic search strategies.

Material and Methods

Study Species and Set-up

The Red Honey Ant, *Melophorus bagoti* (Lubbock), is widespread in the semi-arid grassland deserts of Central Australia. Its habitat is characterised by clumps of the invasive Buffel Grass *Cenchrus ciliaris*, interspersed with *Acacia* spp. and *Hakea eyreana* shrubs and the occasional large *Eucalyptus* spp. tree. Foragers of this species venture out of the nest in the heat of the day (Christian & Morton 1992) and forage for dead insects, sugary plant excretions and seeds (Muser et al. 2005; Schultheiss et al. 2010). In its harsh desert habitat, *M. bagoti* does not use chemical trails to guide foragers. Instead, each single forager is able to find its way around by using both visual navigation and path integration (Cheng et al. 2009).

Experiments were conducted in the natural habitat, as it is important to observe behaviours in the environment in which they evolved to perform best. The field site is located ca. 10 km south of Alice Springs, Australia; data were collected in February and March 2010. The immediate area around one nest of *M. bagoti* was cleared of vegetation, and four feeders (plastic tubs with biscuit crumbs) sunk into the ground due north, east, south and west, at a distance of 3 m from the nest entrance (Fig. 1a, b). Foraging ants were trained to the feeders for a minimum of two days. During this time, they learned the visual cues around the nest and performed many foraging trips. For a test, ants were trapped in the feeders and the nest entrance was covered with a wooden board (ca. 1.2 × 1.2 m). Thus, both the nest entrance and any associated odour cues were covered. The board surface was always covered with a thin layer of sand (glued to the board) and sand was also placed over the edges of the board, so that the floor surface would appear quite homogenous to the searching ants. The trapped ants were then released one at a time, and their paths recorded as

they searched for the nest entrance. Only ants that still carried a food item were recorded and each ant was tested only once. Recording was facilitated by a grid on the ground made of tent pegs and string (3×3 m). We recorded search paths of ants under two different conditions: In the first, the visual panorama around the nest remained unaltered ('open'). It was dominated by close bushes on the western and southern sides, but was very low and open on the northern and eastern sides (Fig. 1c). In the second condition ('cluttered'), we added several artificial landmarks on the northern and eastern side, thereby increasing the overall visual clutter around the testing area (Fig. 1d).

IDF Mapping

We documented the visual surround of the nest using slightly modified methods of Zeil et al. (2003). For each condition, a total of 48 panoramic (360°) photographs (plus one reference photograph taken at the nest entrance) were taken in an octagonal area of ca. 4 m diameter around the nest entrance. Image locations were arranged along 8 radial lines (Fig. 1b), and orientation was kept constant over all images. To eliminate colour shifts due to changing lighting conditions or shade, these images were then transformed into binary black-and-white images. Their resolution was decreased to 5° (Fig. 1e, f) so that they would not hold more information than would be available for foragers of *M. bagoti*, which have an average visual resolution of 3.7° (Schwarz et al. 2011). A pixel-by-pixel comparison of each image to the reference image (taken at the nest entrance) then yielded numerical values of the difference between the two images. These can be displayed as a function of their spatial position in the experimental area, thereby providing what we call here the Image Difference Function (IDF; see also Zeil et al. 2003; Stürzl & Zeil 2007 for more detailed information). Separate IDFs were created for the two experimental conditions.

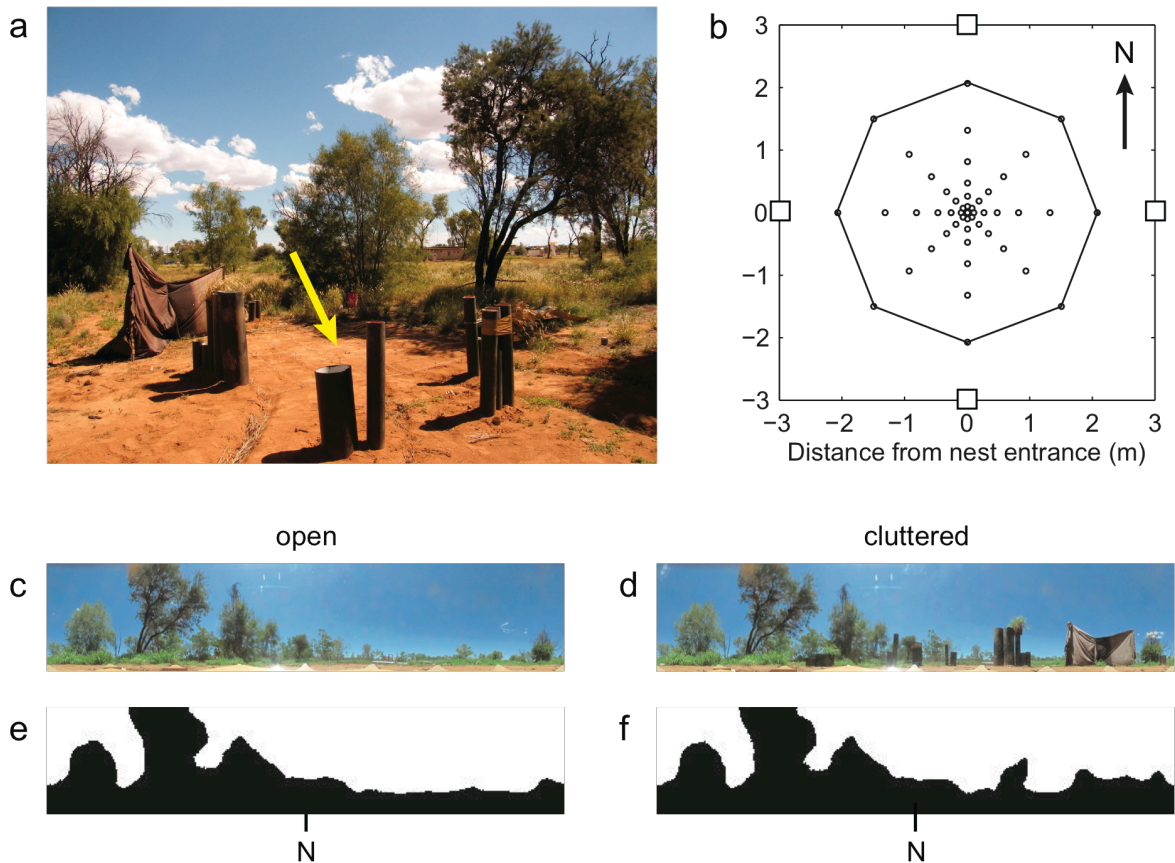


Figure 1: Documenting the visual scenery around the nest entrance. (a) Overview of the experimental set-up, viewed from approx. north-northeast. The set-up is shown in the 'cluttered' condition, and the added landmarks are clearly visible in the foreground. The location of the nest entrance is marked by a yellow arrow. (b) Schematic of the test area with the nest entrance at the centre. The four squares at the outer edges mark the locations of the feeders. Radiating outward from the nest entrance, several panoramic photographs were taken (locations are marked by small circles). (c) Panoramic (360°) picture taken at the nest entrance in the open condition. Note that some of the added landmarks are hardly noticeable in front of the vegetation. (d) Panoramic picture taken at the same location in the cluttered condition. (e),(f) The same images as shown in (c),(d), with the resolution reduced to 5°, and transferred into binary black-and-white images. N marks north.

Search Path Analysis

The search paths were digitised according to their turning points. These were defined as follows: the change in direction has to be at least 45°, the turn has to be completed within a radius of 0.1 m around that point, and the distance to the next point has to be at least 0.1 m. As changes in direction were usually abrupt, this method retains most of the information while simplifying the paths by breaking them down into series of straight movements (segments). Previous work has shown that this method delivers robust and repeatable results for the digitisation of search paths in *M. bagoti* (Schultheiss & Cheng 2011).

We compared search paths of ants in the two conditions in regard to (1) average distance from the nest (as a measure of spread), (2) segment length and (3) turning angle between segments. Segment length was defined as the shortest distance between two turning points, and turning angle as the deviation from the straight direction. To test if maximum search extension corresponds to similar IDF values in both groups, we analysed the data in the following manner: The testing area was divided into 8 sectors, with each sector having a radial line of panoramic images (Fig. 1b) as its midline. For each ant, the maximum distance from the nest was determined in each sector, and the corresponding IDF value at that distance noted. These values were then averaged for each individual. Unless otherwise specified, all comparisons between groups were made using repeated-measures ANOVA.

We investigated the movement pattern of searching ants by looking at the segment length frequency distributions (combining all ants from both the ‘open’ and the ‘cluttered’ condition), and finding the best fitting exponential and power law models. We analysed our data with the method of Edwards et al. (2007). This uses the raw, unbinned data, from which maximum likelihood estimates (MLE) of model exponents are derived. This procedure also allows for the calculation of confidence intervals and for model evaluation by goodness-of-fit tests (G-test with Williams’s correction; Sokal & Rohlf 1995). We fitted single function exponential and power law models to the complete data series. Distributions of exponential models follow

$$f(x) = \lambda e^{-\lambda x} \quad (1)$$

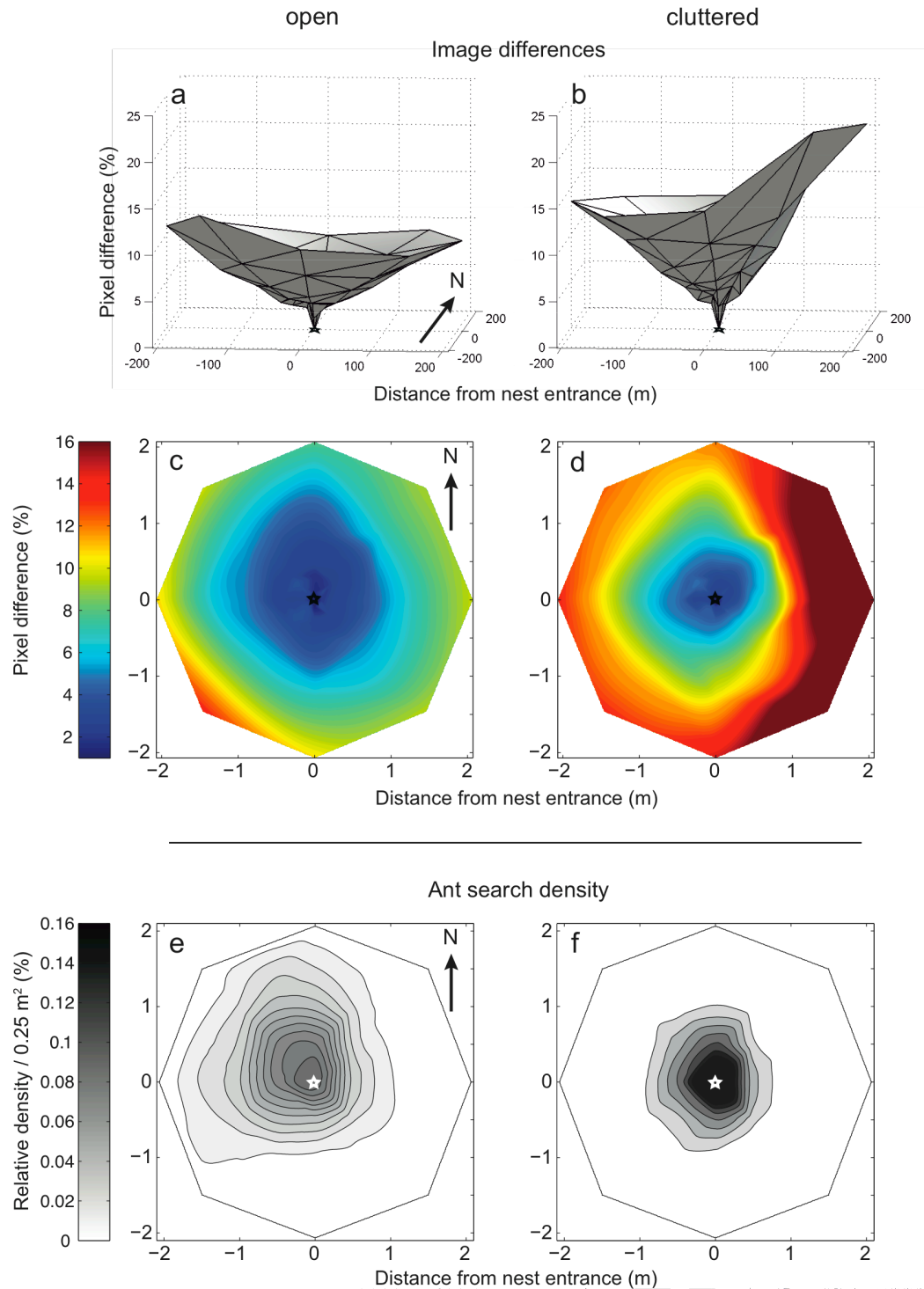


Figure 2: Quantification of visual changes in the test area, and the ants' behavioural response to these changes. N marks north. **Left** shows the open and **right** the cluttered condition. (a-d) These maps were created by comparing panoramic pictures taken around the nest with a reference picture taken at the nest location (denoted by a black star). (a),(b) Three-dimensional image difference functions (IDF) of the test area in the two conditions. Mismatch levels were interpolated between the locations where pictures were taken (triangle-based cubic interpolation). (c),(d) Two-dimensional, colour-coded IDFs of the test area. (e),(f) Density plots of the ants' search paths; the nest entrance is denoted by a white star (open: $n = 70$, cluttered: $n = 58$).

and those of power law models follow

$$f(x) = x^{-\mu} \quad (2).$$

Edwards (2011) also suggests considering models that have an upper bound, as these should be more meaningful for biological data. For the tail end of the distribution we also explicitly tested for the existence of a Lévy walk strategy, as evidence of this particular strategy has been found in searching honeybees *Apis mellifera* (Reynolds et al. 2007a). Lévy walks are characterised by a ‘heavy-tailed’ power law distribution of segment lengths (see Equation 2), where the model exponent is $1 < \mu \leq 3$ (Viswanathan et al. 1999). A more detailed description of the model fitting procedures can be found elsewhere (Supplementary Material of Schultheiss & Cheng in press).

Results

Open vs. Cluttered Visual Scenes

In a first step, we quantified the visual changes an ant would experience when moving around in the test area, and verified that our experimental manipulations exerted a notable effect on the scenery. In both conditions, the IDFs (Fig. 2a-d) showed an increasing change in the visual panorama when moving away from the nest entrance. The increase in image difference was smooth and did not level off at the outer edges of the recorded area. The rate of increase was steeper in the cluttered condition than in the open condition and it reached higher values (compare Figs. 2a and 2b).

In a second step, we looked at the properties of ant search paths that were displayed under these conditions. These were centred on the location of the nest entrance and were made up of loops that bring the ants back to this location repeatedly. The amount of information in the scenery around the nest had a marked influence on the search spread (Figs. 2e, f and 3). Increasing the visual clutter led to searches with a smaller spread ($F_{1,109} = 42.6$, $p < 0.001$). These tighter searches were also characterised by shorter segment lengths (mean: 38 cm for open, 33 cm

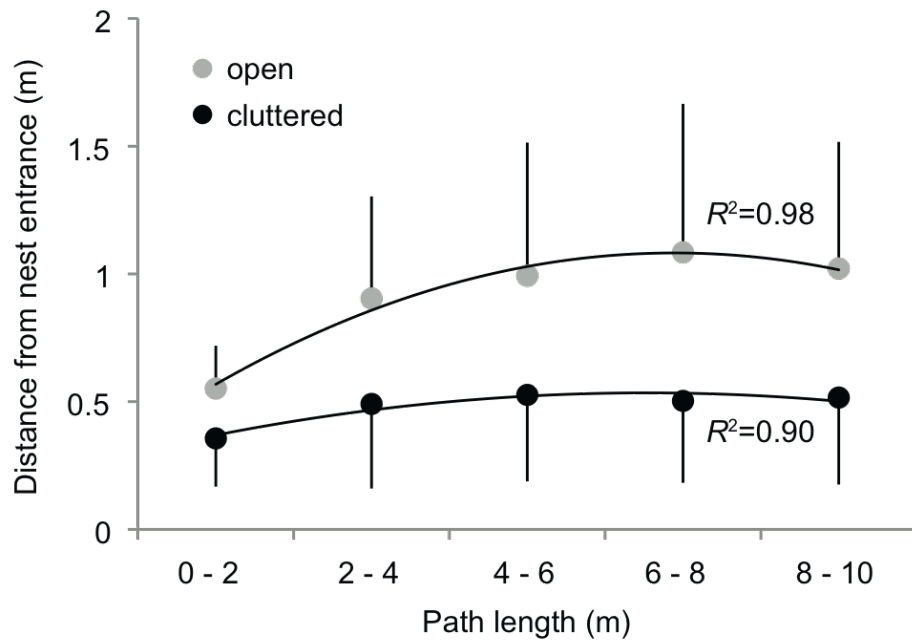


Figure 3: Spread of search in the first 10 m of search path, averaged over the two groups ('open' and 'cluttered'). Data points show average values, error bars display the s.d., and black lines show best fitting quadratic functions. Only paths of 10 m or more in length were considered (open: $n = 62$, cluttered: $n = 49$).

for cluttered condition; $F_{1,83} = 9.6$, $p < 0.01$) and larger turning angles (mean: 101° for open, 111° for cluttered condition; $F_{1,83} = 23.4$, $p < 0.001$; paths were measured over the first 28 segments or 27 turning points, and paths with fewer segments/points were excluded from the analysis; open: $n = 51$, cluttered: $n = 34$). While most of the search is centred almost exactly on the nest location, a slight skew is also apparent in the search density plots (Fig. 2e, f), especially in the ‘open’ condition (Fig. 2e). This skew, which tends towards the north and west in the ‘open’ condition and to the north and south in the ‘cluttered’ condition, seems to match the areas of low image difference in the corresponding IDFs (Fig. 2c, d). However, image differences alone cannot fully explain the ants’ behaviour. Overall, ants in the cluttered condition expanded their search into areas with higher image difference values than ants in the open condition ($t(124) = -6.15$, $p < 0.01$; open: $n = 69$, cluttered: $n = 57$).

Search Expansion

As the search progressed, the pattern of movements made by the ants changed: searches began very close to the nest entrance, and gradually expanded to cover larger areas (Fig. 3; averaged over the whole group). This increase in spread is significant in both conditions (open: $F_{1,61} = 39.4$, $p < 0.001$; cluttered: $F_{1,48} = 11.0$, $p < 0.001$), and is characterised by both a linear trend (open: $F_{1,244} = 110.9$, $p < 0.001$; cluttered: $F_{1,192} = 24.9$, $p < 0.001$) and a quadratic trend (open: $F_{1,244} = 43.4$, $p < 0.001$; cluttered: $F_{1,192} = 14.8$, $p < 0.001$).

Movement Length Distribution

Finally, we investigated the movement pattern of foragers as they were trying to find the nest entrance in the familiar visual surround, by finding a model that adequately describes the data. Figure 4 provides an overview of the data and shows the frequency distribution of movement (segment) lengths over bins of equal size. The fit of exponential and power law models to the segment length distribution is shown in Figure 5 and statistical measures of the model fits are collected in Table 1. This includes the Akaike Information Criterion (AIC), the AIC weights, and the evidence ratios, which are all measures calculated for model selection (Burnham &

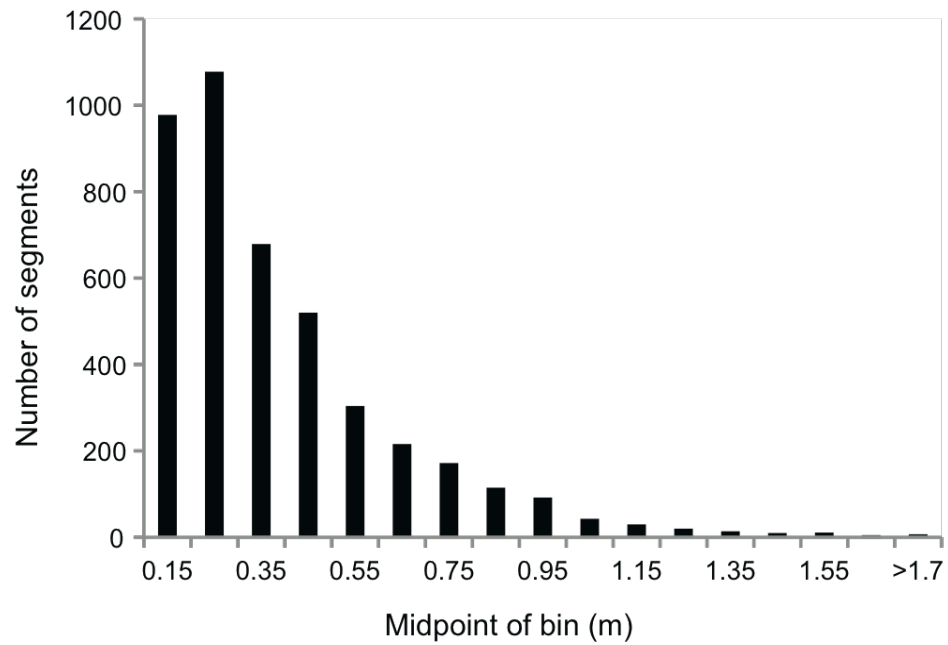


Figure 4: Overview of the segment length frequency distribution. Data were put into bins of 10 cm width, starting at the minimum segment length of 10 cm (segments $n = 4294$).

Anderson 2002). The lowest AIC and a high AIC weight relative to other models indicate the preferred model. For each model, the evidence ratio gives the relative likelihood of being the best. As can be seen in the binned data series (Fig. 4), there are fewer segments in the first bin than in the second bin, although both bins have the same linear size. This ‘positive slope’ in the frequency of very short segments may reflect a genuine trend in the ants’ movements, such as an intermittent small-scale search at the exact nest location, or may result from a systematic sampling error in our methods; a similar pattern was also found in food searches of *M. bagoti* (Schultheiss & Cheng in press). However, positive slopes in the segment length distribution make no theoretical sense, as all searching models expect longer segments to occur with lower frequency. For our model fits, we therefore considered only segments of 0.2 m or more in length ($n = 3316$). Results of the MLE analysis show a strong preference of exponential models over power law models, with the unbounded model faring slightly better than the bounded model (Table 1). A G-test shows that this unbounded single exponential model explains the data adequately ($G = 5.2$, $p = 0.267$). Calculating model fits for the long end of the distribution only (starting at $a = 0.8$ m; $n = 347$) leads to similar results, with the exponential models being preferred over the power models (Table 1). Also, power law exponents are outside the range of Lévy walks (Table 1, bottom).

Table 1: Statistical parameters of function fits in Figure 5. Calculation of maximum likelihood estimates (MLEs) of model exponents follows Edwards et al. (2007) and Edwards (2011). 95% confidence intervals (CI) were calculated with the profile likelihood-ratio test (Hilborn & Mangel 1997), AIC with correction term (AICc), AIC weight, and evidence ratio were calculated following Burnham & Anderson (2002). The tail end of the distribution begins at $a = 0.8$ m. Exp = exponential, ExpB = bounded exponential, PL = power law, PLB = bounded power law

	exponent	95% CI	log-likelihood	AICc	AIC weight	evidence ratio
Fit to whole series						
Exp	$\lambda_{MLE} = 3.832$	3.704–3.964	1139.056	−2274.114	0.650	1
ExpB	$\lambda_{MLE} = 3.828$	3.699–3.961	1139.440	−2272.873	0.350	1.860
PL	$\mu_{MLE} = 2.409$	2.362–2.458	804.903	−1605.808	$4.923 e^{-146}$	$1.321 e^{145}$
PLB	$\mu_{MLE} = 2.196$	2.139–2.253	923.225	−1840.442	$4.390 e^{-95}$	$1.481 e^{94}$
Fit to tail end						
Exp	$\lambda_{MLE} = 4.172$	3.748–4.626	148.639	−293.243	0.673	1
ExpB	$\lambda_{MLE} = 4.152$	3.721–4.611	148.862	−291.654	0.304	2.214
PL	$\mu_{MLE} = 5.174$	4.750–5.629	143.145	−282.256	0.003	243.107
PLB	$\mu_{MLE} = 4.986$	4.526–5.471	146.130	−286.190	0.020	34.011

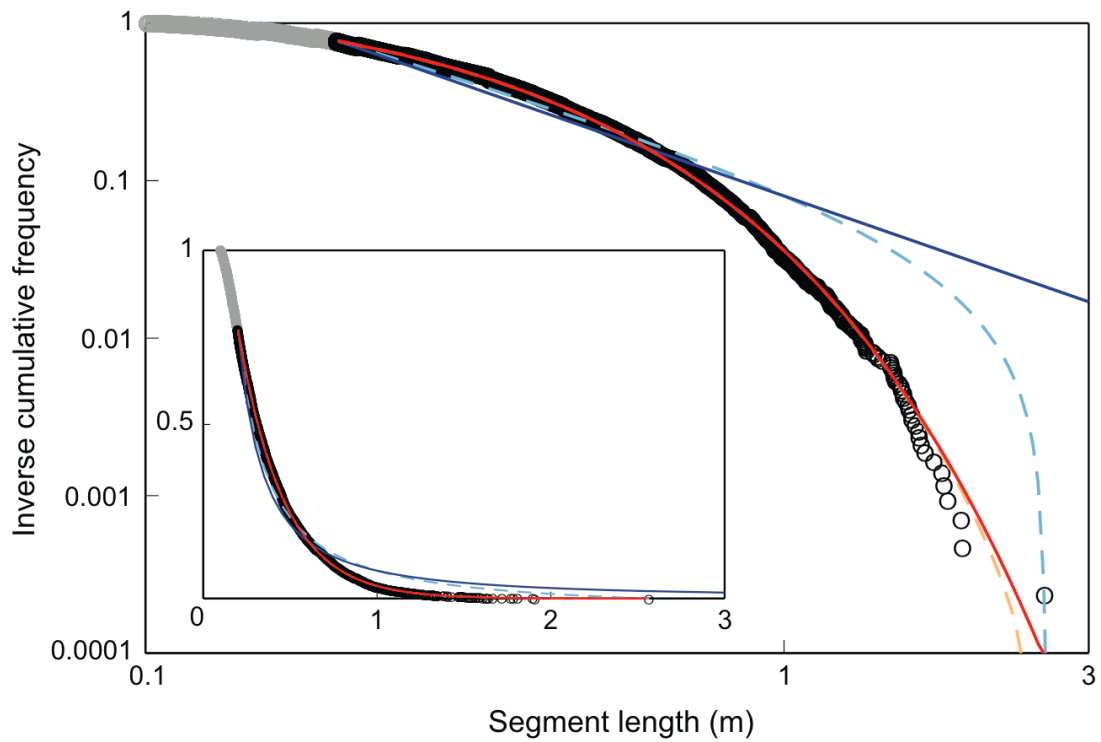


Figure 5: Inverse cumulative distribution of segment lengths; note that both axes are logarithmic. Inset shows the same data series on linear axes. Lines show best fitting models: red = exponential, orange dashed = bounded exponential, blue = power law, light blue dashed = bounded power law. Grey circles show values below the critical segment length, and were not included in the model calculations.

Discussion

We subjected searching *M. bagoti* ants of the same nest to two different visual environments: an open, natural setting and a cluttered setting with added visual landmarks. While the testing area itself remained clear of any objects, these settings differed in the amount of visual information they conveyed. After foragers had become familiar with their visual environment, the nest entrance was blocked. In both conditions returning foragers displayed a search which was centred on the nest entrance location. We analysed these searches in regard to the visual information content of the environment, and in regard to search characteristics that have previously been observed in unfamiliar environments.

Search and Visual Information

In visually guided insects, nest searches are influenced by visual cues: when size and position of landmarks are modified, searches for the nest are altered (Wehner & Räber 1979; Durier et al. 2003; Narendra et al. 2007). Here, we show that a visual panorama with richer information allowed ant foragers to display a tighter and therefore more accurate search (Figs. 2e, f and 3). Foragers achieved this by both increasing their turning angles and decreasing the length of segments in their search paths. From the IDF maps of the test area (Fig. 2a-d) it is evident that the visual surround of the cluttered condition changed with a much steeper gradient than that of the open condition; to achieve the same amount of change the ants had to move considerably longer distances in the open condition. Thus, the ants increased their search accuracy by making the most of the available visual information. However, the IDFs of the experimental areas in the two conditions are not entirely concentric (Fig. 2c, d) and neither are the density plots of searching ants (Fig. 2e, f). In fact, the shapes of the ants' search distributions appear to match the irregular areas of low pixel difference in the IDFs nicely. Hence, it may even be possible to see the influence of structural details from the visual environment on the ants' searching behaviour.

However, it also becomes clear that our way of quantifying the panoramic visual information (using IDFs) cannot fully explain the ants' searching behaviour. Their searches did not extend to the same IDF values in both conditions, which shows that the size and shape of the search pattern do not depend on image differences alone. There are two main reasons why our image difference distributions do not provide a full model of real ants' behaviour: First, image differences provide much-simplified representations of changes. All the variation between images is reduced to pixel differences, and colour differences are not considered at all. Also, this approach only deals with differences in static cues, but not with dynamic cues like motion parallax and optic flow. For instance, visual objects that are hard to discern from the background vegetation may be clearly visible to the moving animal (see Fig. 1d). Insects may pay attention to a whole palette of features such as the colour (Cheng et al. 1986; Cheng 1998), location of edges (Harris et al. 2007), spots of light or centre of gravity of objects (Ernst & Heisenberg 1999; Horridge 2005). Second, there is a profound lack of knowledge as to how ants process visual information when they are searching for the nest. Several models that do not depend on image difference distributions have also been proposed, such as the original snapshot model (Cartwright & Collett 1983), the use of a visual compass (Graham et al. 2010; Wystrach et al. 2011b), or skyline height comparison (Wystrach et al. 2012). Image difference distributions thus provide a useful tool for quantifying the available visual information within an area, but may not reflect the way ants are using views to search for their nest.

Flexibility in the Systematic Search

As the foragers were searching for the nest in the familiar environment, their search paths had a notably smaller spread and much shorter segment lengths than what has previously been reported from *M. bagoti* in a test-field, where foragers were surrounded by unfamiliar visual scenery (Schultheiss & Cheng 2011). However, even in a familiar environment, some flexibility was retained. As the search paths progressed in each condition, they expanded slightly, covering a larger area. This

expansion was much more pronounced when visual clutter was reduced (Fig. 3). The same kind of dynamic search pattern is also displayed in unfamiliar environments, where the rate of expansion is even greater (Figure 4 in Schultheiss & Cheng 2011).

Although nothing is known about the underlying physiological mechanism, Wehner & Srinivasan (1981) have devised a theoretical model that could explain this behaviour. It assumes that ants are able to base their searching behaviour on probabilistic calculations, and that they can keep track of changes in the probability distributions. The beginning of a nest search should then reflect an *a priori* Gaussian probability density function, where the expected goal position corresponds to the peak of the distribution and is thus visited most often. The probability of finding the goal then gradually decreases with the amount of time spent searching in that area. Eventually, this constantly changing *a posteriori* density function will have higher values at the unexplored edges of the area than at the original goal location. The ants then shift their search into these new, unexplored areas, thereby increasing the search spread. Our results show that the size of this search spread (the width of the probability density function in the model) is influenced by the type and the amount of information conveyed by the surrounding visual scenery. An unfamiliar scene holds no navigationally relevant information, and the spread is large. A familiar but fairly open scene holds some relevant information, and the spread is decreased. A familiar and highly cluttered scene holds more information, and enables the forager to restrict the search to an even smaller area.

Movement Patterns: Different Strategies in Familiar and Unfamiliar Environments?

In the present study, searching foragers were very familiar with the visual environment. The ants' segment lengths did not exceed 3 m, and their movement length distribution is well described by a single exponential function, indicative of a random walk strategy like the Brownian walk (Fig. 4 and Table 1). However, on unfamiliar terrain, segments are up to 10 m in length, and their distribution is best described by two different exponential functions that are fit to the short (< 3 m) and long (> 3 m) end separately (Schultheiss & Cheng 2011). (A cautionary note should be added here that this conclusion was drawn from a different kind of analysis; an MLE analysis was not performed in that study.)

In light of the new data presented here, we believe that *M. bagoti* may generally employ a single exponential search strategy to locate a single goal like the nest entrance. Further confirmation of this pattern, however, is needed because all the data in the present study were collected at a single nest of *M. bagoti*. When familiar landmarks are present, the ants can assume they are searching in the right place. Thus, they will continue with the same strategy, which keeps them close to the presumed goal location. In sense of the model of Wehner & Srinivasan (1981), the ants' search would be based on a single Gaussian *a priori* probability distribution function. Similarly, *M. bagoti* ants searching for a single food source at the end of their familiar outbound route also use a single exponential strategy (Schultheiss & Cheng in press). If, however, the visual surround is unfamiliar, ants will be confronted with conflicting information. On the one hand, the release point is the most likely location of the nest entrance, and this is where the ants centre their search path (Schultheiss & Cheng 2011). On the other hand, the unfamiliar visual cues will tell the ants that they are searching in the wrong place. We suggest that the resulting double exponential strategy is then a mixture of two separate search strategies (corresponding to an *a priori* function that is a mixture of two different functions). The first strategy contributes shorter segments, and is used to keep the ants close to the release point; the second contributes longer segments, and is used to bring the ants into unexplored areas, where familiar visual cues may be found.

Movement Patterns: No Indication of Lévy Walks for Desert Ants

Our final analysis investigates the possible existence of Lévy walk characteristics in the movement length distribution of searching ants. Lévy walks have been suggested as a common search strategy in all central-place foragers (Reynolds 2008; Reynolds & Rhodes 2009). They are characterised by a power law distribution with a 'heavy' tail; i.e., a fairly large number of long segments, such that the exponent $-\mu$ (the slope) of the power law function is $1 < \mu \leq 3$, and they can be close to optimal under certain conditions (Viswanathan et al. 1999). Our results suggest that *M. bagoti* foragers do not perform Lévy walks when they are searching for their nest entrance. The ants' movements do not follow a power law distribution

(Table 1), and estimates of μ in the tail end of the distribution (where Lévy characteristics would be most pronounced) are well outside the Lévy range ($\mu = 5.17$ and $\mu = 4.99$, Table 1). As stated before, we need to be cautious when generalising our findings, as all data are derived from a single nest. So far, our results are in line with other findings in this species (Narendra et al. 2008; Schultheiss & Cheng 2011, in press), but are in contrast to findings in honeybees that have been shown to use Lévy walks when searching for the nest (Reynolds et al. 2007a) or a feeder (Reynolds et al. 2007b). However, these bee studies were conducted in a wide-open field with almost no visual landmarks. In contrast, the natural environment of *M. bagoti* always contains visual cues, familiar or not. It is possible that Lévy searches are only used in featureless environments, where no information can be derived from the visual panorama (Sims et al. 2008). Also, the mechanism that produces Lévy movements in flying honeybees may not operate in walking animals.

Conclusion

In the harsh desert environment of *M. bagoti*, it is crucial that each forager is able to find the nest entrance efficiently. In order to achieve this task, the size and shape of foragers' search patterns are influenced by several different processes. With information from the familiar visual environment, foragers are able to constrain their search to a small area around the nest entrance. We have shown that the accuracy of these searches depends on the amount of information that can be derived from the visual scenery. However, even in a familiar visual environment, the systematic search remains dynamic, and gradually expands. Contrary to the 'double' search strategy displayed in an unfamiliar environment, the search paths observed here in the familiar nest surround can be modelled as a single exponential strategy, which is similar to a Brownian walk. Thus, foragers of *M. bagoti* use information from the visual environment to adapt their search strategy.

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CONCLUSION

The work presented in this thesis provides details on the foraging ecology of the Australian desert ant *Melophorus bagoti*. As part of an effort to study navigation in several desert ant species, *M. bagoti* has gained significant momentum over the last decade and is establishing itself as a new model species (Cheng et al. 2009). This attention stems not only from its ecological equivalence with well-established model species from the genus *Cataglyphis* (Wehner et al. 2003) but equally (and arguably more importantly) from its differences to these species, especially in its choice of habitat. While these differences open the door for studying the effects of environment on navigational capabilities, they also call for intimate knowledge of ecological details in these species.

Part of this study described the foraging behaviour of *M. bagoti* on the colony level, where previously information was lacking. Unusual among desert ants, foragers are able to use recruitment for food retrieval. The remainder of this study focused on the searching behaviour of foragers, and the influence of environmental cues. In themselves, search paths are highly structured in a way that enhances searching efficiency. Additionally, foragers glean detailed information from a variety of environmental cues and fine-tune the path structure to the specific requirements of the search.

Colony-level Foraging Traits

Being a thermophilic desert ant (Christian & Morton 1992), the foraging activity of *M. bagoti* is restricted to a window of ca. 50–70°C soil surface temperature. Daily activity profiles are therefore quite heterogeneous, owing to day-to-day variations in temperature. Foragers are opportunistic scavengers, and dead insects comprise a large part of their diet. In these regards, *M. bagoti* is very similar to other thermophilic desert ants (Marsh 1985; Schmid-Hempel 1987). In others it is quite different, as in the use of grass seeds as a food source and in its ability to recruit nestmates to

lucrative food sources. The ability to recruit reveals that foragers are not entirely solitary, but have the capacity for cooperative food retrieval. It also demonstrates that foragers have the means to transfer information about certain localities between individuals. This system could arguably be used for other navigational tasks as well, and may have to be considered in other studies. However, the mechanism by which information on the food location is transferred to the recruited ants remains poorly understood, and requires further research. Most ants use pheromones for mass recruitment (Hölldobler & Wilson 1990), and *M. bagoti* certainly seems to have the capacity, as shown by its nest relocation behaviour. But generally, desert ants make very limited use of pheromones outside the nest (Wehner 1987; Cheng et al. 2009). Furthermore, the results that could be obtained in *M. bagoti* indicate no use of pheromones during recruitment, and their behaviour appears to be inconsistent with known recruitment mechanisms.

Ecology of Searching Behaviour

Searching behaviour in *M. bagoti*, while seemingly rather simple and static, is in fact highly complex and variable. The basic path structure for locating a single target, a food source or the nest entrance, is a looping search that is centred on the estimated target locality, ensuring that this location is visited most frequently. The size (spread) of search paths is flexible, and is governed by the current level of knowledge the forager has about the target location. As a consequence, searches are not only dynamic over time as the forager accumulates information from previous experiences, but also fine-tuned to any given situation with information from the outside environment. In a foraging scenario, *M. bagoti* foragers adjust their search spread to the natural distribution patterns of different food types, most likely either by selectively memorising foraging experience or by exploiting physical differences in odour cues. Further experiments are needed to explore this question in more detail. In a homebound scenario, foragers rely heavily on familiar visual (landmark) cues to find the location of the nest (Narendra 2007b). The arrangement of these cues informs the forager of the whereabouts of the nest entrance, and intriguingly, search accuracy is increased when more visual information is provided. But visual cues are

not the only source of information for searching foragers. Their knowledge of the nest position is also based on information from their path integration system (Narendra 2007a), which becomes less accurate the longer it runs (Müller & Wehner 1988; Sommer & Wehner 2004; Merkle et al. 2006). Taken together, these results show that searching behaviour of *M. bagoti* is deeply entwined with its foraging ecology and its navigational toolkit.

Optimal Search Theory

The measure of search spread is a useful proxy that can help us understand how important different kinds of information are for searching ants, but it does not illustrate how a search path is structured. In a simplified manner, a searching ant has to decide in what direction and for what distance it will move, over and over again. Thus, a search path is a long series of straight movements interrupted by reorientation events. Simulation studies have shown that movement length is an important trait that determines the success rate in different searching scenarios (Bell 1991). Based on different movement length frequency distributions, several ‘optimal’ models have been devised. Several studies have since shown that movements of searching animals often follow similar relationships. Since the formulation of the Lévy walk in the 1980s (Shlesinger & Klafter 1986) this has become something of a ‘hot topic’, leading to significant advances in analytical methods (Edwards et al. 2007; James et al. 2011). While evidence for Lévy walks in nature remains sparse (Edwards 2011), they have been described in honeybees *Apis mellifera* (Reynolds et al. 2007a; Reynolds et al. 2007b; Reynolds et al. 2009). Although foraging characteristics of bees and ants are similar, the results presented here show that search paths of *M. bagoti* have characteristics of a different strategy, the Brownian walk. Furthermore, analysing search behaviour in different contexts revealed an intriguing relationship: foragers use different strategies for nest searches in familiar or unfamiliar settings. In the presence of familiar visual cues, which provide information for pinpointing the nest, they search with a uniform Brownian walk. In the absence of such cues, their movement lengths follow a non-uniform distribution as if they were a composite of two separate Brownian walks. This composite strategy results in

movements that are much longer, leading to search paths with much greater spread. Once more, these results demonstrate how the structure of search paths is tailored to the environmental requirements. All available information is used by foragers to improve searching performance.

Where to from here?

Desert ant foragers are ideal test subjects for the study of searching behaviour. They live in nests, and there is always a ready supply of new subjects; they forage solitarily, enabling the study of individual behaviours; they are small, which makes their movements relatively easy to follow; and their movements are confined to two dimensions, which greatly facilitates the recording of behaviours. Even with simple experimental set-ups, searching behaviour can be studied in detail.

This study has revealed several different strategies that shape an ant's search path. Here, they are investigated separately, but they probably work in unison. Further experiments with *M. bagoti* could investigate if each system continues to work under different circumstances, e.g., if the length of the path integration vector also affects nest-searches in familiar visual surrounds and food-searches, or if the amount of visual information also affects the accuracy of food-searches.

Comparative studies with other solitary foraging desert ants should prove particularly revealing. These ants can be found in different areas of the world (Wehner 1987) and occupy the same ecological niche as *M. bagoti* (Wehner et al. 2003; Cheng et al. 2009). Some species, like the North African *Cataglyphis fortis*, inhabit featureless salt pans (Wehner 1987; Dillier & Wehner 2004), which provide a very different visual environment to that of *M. bagoti*. Differences in navigational behaviour (Bühlmann et al. 2011) and learning ability between the two species (Schwarz & Cheng 2010) are probably due to these habitat differences. The searching strategies of desert ants in featureless environments may also be markedly different, and are certainly worth investigating. Preferably, the searching behaviour of *M. bagoti* should be compared with a closely related species to minimise the influence of phylogenetic differences. Within the genus *Melophorus*, a suitable species (one that inhabits featureless deserts and is a solitary forager) has yet to be identified, but may be found in the dry salt lakes of South Australia (see

Mitchell 1973). The searching behaviour of these two *Melophorus* species could further be compared with that of *Cataglyphis*, where a similar species pair is given by *C. bicolor*, which inhabits quite cluttered environments, and *C. fortis*, which lives in salt pans.

While this line of research would provide an excellent understanding of adaptive patterns in searching behaviour, the true challenge lies in understanding the processes that create these patterns. How does an ant decide when and where to turn? How does she perceive, filter and process cues to inform those decisions? How does she integrate memories? The relative simplicity of an ant's brain offers a realistic possibility to study these physiological mechanisms down to the cellular, or even the molecular level.

Résumé

Over the last decades, solitary foraging desert ants have proven very useful for the study of navigational processes. They are equally well suited for studying the processes of searching behaviour, and both topics are in fact closely interwoven. This study explores the search behaviour of *M. bagoti* foragers in detail, and uncovers several strategies that shape the structure of the search path. By exploiting several sources of information, foragers ultimately display search paths that are adapted to the environmental context. To investigate if these strategies are adaptations to the comparatively complex environment of *M. bagoti*, comparative studies with other desert ant species should prove enlightening.

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APPENDIX I

Appendix I contains Chapters II and IV in their published form:

- Schultheiss, P., Schwarz, S. & Wystrach, A. 2010. Nest relocation and colony founding in the Australian desert ant, *Melophorus bagoti* Lubbock (Hymenoptera: Formicidae). *Psyche*, 2010, 435838.
- Schultheiss, P. & Cheng, K. 2011. Finding the nest: inbound searching behaviour in the Australian desert ant, *Melophorus bagoti*. *Animal Behaviour*, 81, 1031-1038.

Research Article

Nest Relocation and Colony Founding in the Australian Desert Ant, *Melophorus bagoti* Lubbock (Hymenoptera: Formicidae)

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Even after years of research on navigation in the Red Honey Ant, *Melophorus bagoti*, much of its life history remains elusive. Here, we present observations on nest relocation and the reproductive and founding stages of colonies. Nest relocation is possibly aided by trail laying behaviour, which is highly unusual for solitary foraging desert ants. Reproduction occurs in synchronised mating flights, which are probably triggered by rain. Queens may engage in multiple matings, and there is circumstantial evidence that males are chemically attracted to queens. After the mating flight, the queens found new colonies independently and singly. Excavation of these founding colonies reveals first insights into their structure.

1. Introduction

The Australian desert ant, *Melophorus bagoti* Lubbock, is a widespread species of arid Central Australia. It inhabits low-shrub and grassland deserts, where it builds fairly large underground nests [1]. The outdoor activity is mainly restricted to the hotter summer months, when the ants are active during the heat of the day. Foragers usually begin their activity at soil surface temperatures of about 50°C and continue to forage at temperatures above 70°C [2]. They forage solitarily for food such as dead insects, seeds, and sugary plant exudates ([3], personal observations) and are well known for their ability to store liquids in the abdomens of specialised workers, the so-called repletes or “honey pots” (hence their common name “Red Honey Ant” and indeed the genus name *Melophorus*, meaning “honey carrier”). This method of food storage is also adopted by several other seasonally active ants, for example, *Cataglyphis* [4] of North Africa, *Camponotus* [5] of Australia, and *Myrmecocystus* [6] and *Prenolepis* [7] of North America (the latter store fat, not sugar).

In the recent years, *M. bagoti* has attracted increasing attention for its navigational abilities (e.g., [8–13]; for a review see [14]), thus making a broader understanding of its behaviour and life history desirable.

2. Materials and Methods

The study site is located 10 km south of Alice Springs, NT, Australia, on the grounds of CSIRO Alice Springs. The area is characterised by an arid climate, with an average annual rainfall of 279.4 mm [15]. The soil consists of sandy flood plain alluvium [16], and the vegetation is a mosaic of *Acacia* low open woodland and *Triodia* low open hummock grassland [17], although much of the latter has been replaced by the invasive Buffel Grass *Cenchrus ciliaris*. *M. bagoti* is common in the area, and their nests occur at a density of ~3/ha, which is much lower than previously reported by Muser et al. [3] from a different location.

The observation of a nest move was made in December 2008, and colony founding was observed between December 2008 and March 2009. As these incidents were unpredictable, observations could not be made systematically. Due to unusually high rainfall in November 2008 (wettest November on record with 156 mm rain), much of the area was covered by fresh vegetation for most of the summer.

3. Results and Discussion

3.1. Nest Move. After a full week of rainy weather, some nests of *M. bagoti* reopened their entrance holes on 21 November

2008. In the following three weeks, 12 of 16 observed nests relocated the position of their entrances several times by 5–191 cm (average: 73 cm). This behaviour is usually displayed much rarer. Occasionally several entrances were in use at the same time. In preparation for other experiments, the area around one of these nests was cleared of vegetation on 25 November whereby a nest chamber very close to the surface was accidentally opened. In the following days, the nest relocated its entrance to this new opening (distance: 47 cm, bearing: 190°), closing the old entrance. On 3 December (partly cloudy, max. temp. 40.9°C) at 17.00 hour we noticed that this nest was in the middle of relocating to a new nest site (distance: 17.75 m, 205°). A continuous but sparse moving column of ants, including repletes, was observed between the two nest sites. The column was directed to the new nest in almost a straight line. Although most workers went from the old to the new nest, some were observed going the other way. The width of the column varied from a few cm to about 1 m but always seemed to consist of distinct trails. Most, but not all of the repletes, were pulled or pushed out of the old nest opening by workers and proceeded to move to the new nest on their own (see Supplementary Material), where some were dragged into the entrance by workers. Because foragers are usually the only ants that leave a nest, repletes are necessarily unfamiliar with the environment around the nest. They must therefore rely on other cues to find the direction and location of the new nest. There are three possible explanations. Other workers within the nest could convey the information, they might simply follow other ants on the trail, or they might use a system of chemical (olfactory) marking. Indeed, on several occasions workers were seen dragging the tip of their abdomens across the sandy soil (see Figure 1 and the Supplementary Material), a behaviour which has not been observed in *M. bagoti* or any other solitary foraging desert ant so far. These ants may be laying intermittent odour trails. If this conclusion holds true, it will have important implications for future studies on the navigational strategies of this ant species.

We could distinguish two types of repletes, as previously described by Conway [1]: ones with clear, amber-coloured abdomens and ones with milky white abdomens. The sizes of their inflated abdomens were variable. One dealate queen was also observed, and one winged male, but no eggs, larvae or pupae. The queen was dragged all the way from the old to the new nest (see the Supplementary Material). All activity ceased at 17.30 hour. Over the next few days we checked for activity sporadically. The old nest was now presumably abandoned. On one occasion some workers and one replete from another nearby nest (distance: 19.98 m) entered the old abandoned nest. However, no further activity was observed at the old nest after this incident. At the new nest excavating activity was at first very high, but during the following days the activity slowed down considerably and eventually came to a stop. The nest reopened on 8 January and remained active until the end of the season.

Although nest emigration behaviour seems to be common in forest-dwelling ant species [18], this does not seem to be the case for *M. bagoti*. Once a nest is established, its location usually does not change over many years (personal

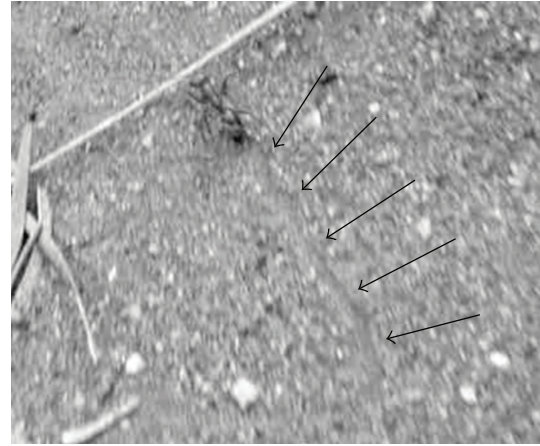


FIGURE 1: A worker of *M. bagoti* dragging her abdomen across the sandy surface during a nest relocation. Arrows indicate the track left behind in the sand. Still photo taken from a film sequence, credit A. Wystrach.

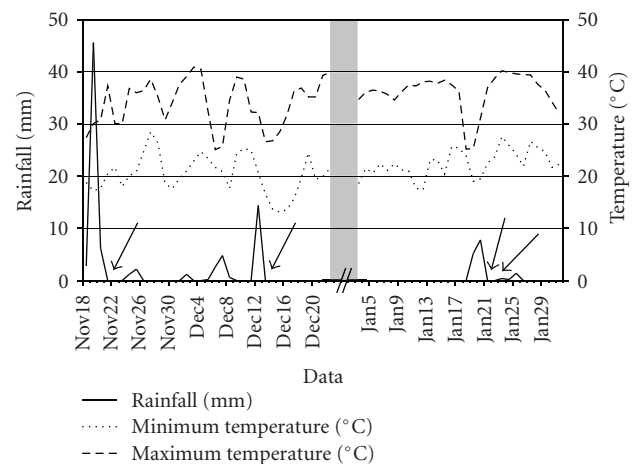


FIGURE 2: Timing of mating flights in *M. bagoti* during the summer 2008/09. Daily rainfall and temperature (min./max.) are shown for the time period from 18.11.08 to 31.01.09, excluding the period from 23.12.08 to 02.01.09 when no observations were made (indicated by grey bar). Arrows indicate observed mating flights. Climate data from [15].

observation). In the described case the move was probably triggered by our disturbance.

3.2. Colony Founding. The founding stage of an ant colony is usually characterised by the same sequence of events. The virgin queen leaves the nest in a mating flight and is inseminated by one or several males. She then looks for a new nest site and starts excavating a small nest, where she lays eggs and rears a small brood [19].

Several nuptial flights were observed during the summer of 2008/09, always after rainy days (see Figure 2) and always in the mornings. Heavy rain is a common trigger for the timing of mating flights in desert ants [19]. Sometimes queens and males left the nest together to fly off, at other

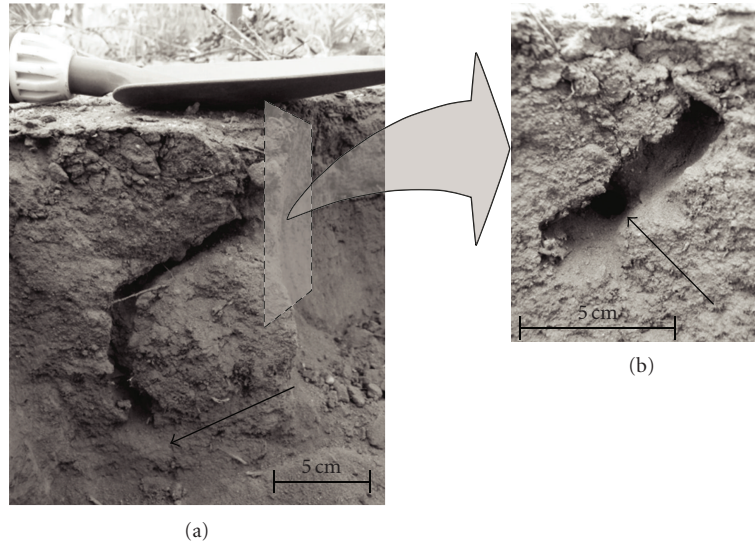


FIGURE 3: (a) Overview of an excavated founding colony of a *Melophorus bagoti* queen. Arrow indicates the location where the dead queen was found. (b) Close-up of the chamber encountered during excavation, the part of the channel leading to the chamber has been removed. Arrow indicates the channel leaving the chamber on the other side; see text for details. Photo credit P. Schultheiss.

times only queens did so. At about 10.30 hour on 21 January 2009, mating flights occurred at four nests simultaneously. As it had rained for the two previous days, it was humid, overcast, and warm (61% RH, 29°C at 9.00 hour). From this synchronised behaviour, we can surmise that mating occurs in swarms, although no such mating site could be located. One mating was actually observed: an already dealate queen was found on the ground, surrounded by several males, of which one copulated with the queen once for a few seconds.

The following day, a dealate queen was observed leaving a nest at 10.15 hour and was followed as she wandered around the area up to a maximum distance of 50 m from the nest entrance, regularly seeking thermal refuge on small plants and twigs. During this time, she copulated once with one male and three times with another male. On both occasions the queen had climbed onto a small plant and remained motionless while the male flew around her. This behaviour is somewhat reminiscent of the sexual calling behaviour of some ponerine ants [20]. The copulations lasted from a few seconds to about half a minute. As all the observed copulations involved dealate queens, they were obviously not regular matings; it seems though that queens readily mate even after they have broken off their wings and possibly even attract males chemically. After 1 hour 50 minutes we stopped following the queen; it is not known if she returned to the nest.

Another dealate queen was seen being followed by a flying insect (probably Diptera, Syrphidae, of which the subfamily Microdontinae has larvae that prey on ants in their nests; the adults are usually found in the vicinity of ant nests [21]). It followed the exact path the ant took at a constant distance of about 10 cm (see the Supplementary Material) until it eventually lost the ant and flew away after searching for a little while.

Queens founded new colonies independently and without the help of other queens or workers (haplometrosis, see [22]); this mode of colony founding is common in formicine ants [19, 23]. However, nothing is known about the number of queens in later colony stages or other populations of *M. bagoti*. For example, in North American ants of the genus *Myrmecocystus*, which can be regarded as the ecological equivalent to *Melophorus* [24], founding queens are often joined by other queens after they have excavated the first nest chamber alone [25]. Also, some desert ants in North America, including *Myrmecocystus*, display considerable geographic variation in their mode of colony founding [26]. We observed a total of 21 dealate queens at their attempts to establish new colonies (all on 21 January). Of these, only five were in a completely open place, while the remaining queens chose a spot in the shade of a little plant or twig. Here the queens started to dig at a shallow angle, using their mandibles (see the Supplementary Material). They continued digging for sometimes several hours. In one case, the queen had chosen a site that was close to an already existing nest (distance: 7.70 m), and workers from this colony apparently attacked and killed the queen. While several workers dragged the dead queen away, one worker closed the hole of the queen rapidly. After two days, 12 of the 21 holes were closed, rising to 15 after another four days; by 10 March, only one remained open (although obstructed by a branch). All colonies can thus be regarded as failed, for reasons unknown. Four of the closed founding colonies were then excavated. Three of these continued as a narrow channel underground for 2–10 cm, ending in a dead end with no remains of the queen, being wholly or partially filled with debris. The fourth hole started as a narrow channel, slowly sloping downward before opening into a small chamber (length: 7.5 cm). This was oriented at a right

angle to the channel but diagonally to the surface, at a depth of 4–9 cm below ground (see Figure 3(b)). The channel then continued downwards at roughly 45° for another 8 cm, turned abruptly downward, and ended without a chamber at a total depth of 16 cm below ground (see Figure 3(a)). Remains of a dead queen were found at the end of the channel, and parts of the channel were filled with debris.

The fact that there was no nest chamber at the end of the channel indicates that the queen died before she had fully excavated the founding nest. Although the observations presented here are necessarily incomplete and many important questions remain unanswered, they do offer a fascinating insight into the early stages of an ant colony.

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Due to copyright laws, the following articles have been omitted from the section Appendix I and Appendix II of this thesis. Please refer to the following citations for details.

Schultheiss, P. & Cheng, K. 2011. Finding the nest: inbound searching behaviour in the Australian desert ant, *Melophorus bagoti*. *Animal Behaviour*, 81, 1031-1038. DOI <http://dx.doi.org/10.1016/j.anbehav.2011.02.008>

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