Foraging ecology of the thermophilic Australian desert ant, *Melophorus bagoti*

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Abstract. The paper describes the foraging ecology of the Australian desert ant, *Melophorus bagoti*, a thermophilic, diurnal scavenger with ground-nesting colonies. Overlapping foraging ranges, low foraging success rates, and intercolony aggression suggest intense competition for food between colonies. Daily foraging starts when soil surface temperatures approach 50°C. Workers search individually and collect predominantly dead insects. Occasionally, they consume plant secretions. Foraging activity peaks on mid-summer days. On cloudy days the onset of foraging is delayed, and the foraging activity is low. Ants do not forage on rainy days. Typically, workers start their above-ground activities with a few short exploration runs. On average, they perform one foraging run on the first day of their outdoor lives. With age they gradually increase foraging site fidelity and daily foraging effort. Individual foraging efficiency is low at the beginning but grows with experience. However, due to a high mortality rate and, hence, high forager turnover, average rates of foraging success for a colony remain rather low. The outdoor activity gradually decreases towards the end of summer and appears to stop completely during the winter months.

Introduction

Thermophilic desert ants from the genera *Cataglyphis*, *Ocymyrmex* and *Melophorus* have been hypothesised to occupy equivalent ecological niches as diurnal scavengers in the Saharan, the Namib, and the Australian deserts, respectively (Wehner 1987). To date, a variety of biochemical, physiological, morphological, and behavioural adaptations have been identified in *Cataglyphis* (Wehner *et al*. 1992; Lighton and Wehner 1993; Gehring and Wehner 1995; Cerdá and Retana 2000; Cerdá 2001), *Ocymyrmex* (Marsh 1985*a*, 1987, 1990; Turner *et al*. 2000), and *Melophorus* (Christian and Morton 1992; Hoffmann 1998; Andersen 2003), which all contribute to the ants' abilities to forage in full sun during the hottest periods of day and year at temperatures at which less heat-tolerant species stop above-ground activity or retreat to cooler places. While *Cataglyphis* and *Ocymyrmex* species have been studied intensively during the past three decades (*Cataglyphis*: e.g. Harkness and Wehner 1977; Schmid-Hempel 1983; Wehner *et al*. 1983; Schmid-Hempel and Schmid-Hempel 1984; Wehner *et al*. 2004; *Ocymyrmex*: e.g. Marsh 1985*b*, 1987, 1990; Wehner 1987), little is known about the foraging ecology of thermophilic ants outside of Africa.

The endemic Australian genus *Melophorus* forms the most abundant group of ants in arid Australia with over 500 species (Andersen 2003), of which less than 10% have been described (Shattuck 1999). All species are polymorphic and thermophilic (Andersen 2000). They are ground nesting, and foraging is strictly diurnal (Shattuck and Barnett 2001).

Melophorus bagoti Lubbock, the focus species of the present account, is an exceptionally thermophilic ant that is widespread in the low-shrub and grassland deserts of arid Australia (Christian and Morton 1992; Andersen 2000; Shattuck and Barnett 2001). A single *M. bagoti* nest may contain over 2800 workers and repletes ('honey pots') of continuously varying body sizes (Conway 1992). There is no clear-cut division of outdoor duties between these polymorphic workers (Christian and Morton 1992). However, the largest workers ('soldiers') often guard the nest by patrolling around the entrance hole (B. Muser, S. Sommer, R. Wehner, unpublished observations), whereas foraging ants are in the lower range of the size distribution. Recruitment behaviour has never been observed (Kohler and Wehner 2005), although the question of recruitment has not been addressed experimentally. Foraging ants search individually. They mostly collect dead arthropods (Christian and Morton 1992). Foraging is strictly diurnal and stops over winter (Christian and Morton 1992; Conway 1992; Shattuck and Barnett 2001). In view of the growing interest in the navigational mechanisms of these ants (Kohler and Wehner 2005; further work from our group is in progress), we felt a need for a deeper understanding of the foraging ecology of this species.

Here we focus on the ontogeny of individual foraging parameters (that is, on foraging effort, site fidelity and foraging efficiency) by recording individually marked ants from the very beginning of their above-ground activities. At the colony level, we extend the knowledge of general foraging characteristics of *M. bagoti* (see Christian and Morton

1992; Conway 1992) by investigating daily activity patterns, taxonomic diet composition, and foraging success.

Among thermophilic desert ants, foraging ecology has been studied most intensively in *Cataglyphis bicolor* of northern Africa (e.g. Harkness and Wehner 1977; Schmid-Hempel 1983; Wehner *et al.* 1983, 2004; Schmid-Hempel and Schmid-Hempel 1984). Here we compare the foraging behaviour and colony characteristics of the two species, *M. bagoti* and *C. bicolor*, on the basis of their strikingly different foraging efficiencies.

Methods

Study site

The study was performed in the West MacDonnell National Park next to the Simpson's Gap Visitor Centre (23.43°S, 133.44°E), 17 km west of Alice Springs, Northern Territory, Australia. The vegetation at this site is dominated by buffel-grass tussocks, *Cenchrus ciliaris*, *Acacia* and *Eucalyptus* trees, and a few *Cassia* shrubs.

At this site the spatial distribution pattern of *M. bagoti* colonies (hereafter referred to by their number, e.g. 'Nest 3') tends towards overdispersion. The mean nearest-neighbour distance (Clark and Evans 1954; Sinclair 1985) between colonies is ~20 m, and the density amounts to ~13 nests per hectare (Kohler and Wehner, unpublished data). Most nests have only one entrance, which is relocated occasionally. The relocation of an entire colony was observed once during the study period (January and March 2003) and extended over 10 days. We never found any evidence for polydomy in *M. bagoti*, although the colony structure has not been investigated systematically.

The following experiments were performed on a randomly chosen subset of colonies, as it was impossible to observe more than one nest simultaneously. The only experiment for which the colony was not chosen at random was the tracking of individual foragers (*Individual foraging activities*, see below).

Colony activities

The composition of the diet of the ants was analysed during two consecutive days at Nest 9 by capturing all successfully returning foragers (*n* = 107) at the nest entrance. The live weight of the ant and the fresh weight of the food were determined to the nearest 1 mg using an analytical balance (Kern, GS 410-3). Food items were classified according to the insect order to which the insect corpses belonged. Other categories comprise unidentifiable insects, plant material, and miscellaneous items including unidentifiable objects. The contribution of liquid food to the diet of *M. bagoti* could not be assessed.

The foraging efficiencies were assessed for Colonies 3, 9 and 10. At each nest all returning ants were counted during one full day. Runs were classified as successful when returning ants carried a solid food item. Ants that had been consuming plant secretions (see below) could not be identified as such, and hence, their foraging runs were classified as unsuccessful. The foraging efficiency was calculated as the number of successful runs divided by the total number of runs per day and colony.

The correlation of foraging activity with daytime and soil surface temperature was investigated at Nests 3, 4, 10 and 11. Start and end of the above-ground activities could be identified easily because the nest entrances were blocked over night with soil particles. At Nests 3 and 10 temperatures and foraging activities were measured once during the peak season (mid-February) and once during the late season (mid-March). Additionally, the impact of low soil surface temperatures on foraging activity was measured on cloudy days at Nests 4 and 11 (beginning of March). For a better comparison between seasons, local standard time was converted into solar time. Foraging activities were recorded as outbound runs per minute. Soil surface temperatures were measured in the sun with the thermocouple covered by a monolayer of sand grains. They were determined to the nearest 0.1°C (Physitemp, BAT-12) at 15-min intervals.

In order to investigate whether any type of recruitment occurred, a basic recruitment experiment was performed at Nest 3. Prior to the experiment all foraging ants (*n* = 102) were marked individually for three days. On the experimental day (Day 4) a feeder containing biscuit crumbs was installed 5 m from the nest entrance ~30 min after the onset of the foraging activity. One observer noted the time of arrival of each ant that visited the feeder for the first time, while another observer recorded the outbound activity at the nest entrance. Activity was spatially divided into feeder activity (that is, the frequency of ants leaving the nest within the 90°-sector facing the feeder) and non-feeder activity (that is, the activity that occurred in the remaining 270°-sector) (see inset Fig. 4). The directions of the outbound runs were recorded at 0.5 m from the nest entrance (that is, when the ants crossed a reference circle of radius 0.5 m). After 2 h the feeder was removed.

Individual foraging activities

Individual foraging events were recorded at Nest 3. This particular nest was chosen because it was in an area where the vegetation was not too dense. This greatly facilitated the tracking of foragers and kept the loss of ants during recording low. The vegetation around the nest was mapped on graph paper at a scale of 1 : 100 with the aid of a 2-m square grid of strings that was laid over an area of ~42 m × 52 m. All foraging ants of the focus nest were marked by day-specific colour dots (enamel-colour) for five consecutive days before the start of the recording period (Day 1). Since the rate of unmarked foragers gradually decreased to a constant level of ~25 ants per day during this period, the marking procedure suggested that at Day 1 all unmarked ants were just starting their foraging lives. Because it was impossible to track all the foragers, a randomly selected subset of 25 ants were marked individually by applying a two-colour code (dots painted on alitrunk and gaster), when they appeared at the nest entrance for the first time. This was done with six ants on Day 1, and with one ant, on average, on each of the following days. The remaining new foragers, 25 ± 3 ants per day (mean ± s.e., *n* = 21 days), were continuously marked by a day-specific colour (daily cohorts). During decades of experimentation with desert ants this marking procedure proved to be reliable (that is, it allowed correct identification of individual ants as well as distinction between marked and unmarked individuals).

While one person tracked as many runs as possible (236 runs of the 20 ants; see Results), another observer recorded (1) the times when each focus ant left the nest and returned to it (out- and in-times), (2) the directions of all outbound runs (*n* = 414), and (3) the ants' foraging success (successful versus unsuccessful). In order to determine the directions of the outbound runs a circle divided in sectors of 30° angular width was drawn around the nest entrance (radius: 0.5 m). Out-times and in-times were determined to the nearest minute.

The daily mortality rate (μ) was computed by fitting the exponential survival function

$$N_t = N_0 \cdot e^{-\mu t} \tag{1}$$

to the number (*N*) of resighted (individually marked) ants per day (*t*). The subscripts 0 and *t* indicate the start of an ant's foraging activity and its above-ground age, respectively. The ants' above-ground half-lifetime ($t_{0.5}$) and the size of the forager force (*F*) at Nest 3 were derived from the estimated daily mortality rate. They were calculated as follows:

$$t_{0.5} = \frac{\log_e(2)}{\mu} \tag{2}$$

and

$$F = N_f \cdot \sum_{t=0}^{\infty} e^{-\mu t} \tag{3}$$

where N_f is the number of new foragers per day, and t is the above-ground age (in days) of the different cohorts foraging per day. For the calculation of F (Eqn 3) a constant rate of new foragers per day was assumed ($N_f = 20$, which is ~80% of the daily cohorts; see Results).

Above-ground activity was divided into exploration runs and foraging runs (for a description of exploration runs of *C. bicolor* see Wehner *et al.* 2004). Runs involved in nest maintenance, e.g. nest digging and nest cleaning, were very short (<1 min) and exhibited straight outbound and inbound trajectories. These runs were not recorded systematically.

Individual foraging success rates were calculated directly as the ratio of successful foraging runs to the total number of runs per ant. As exploration runs did not serve any foraging purpose (see Wehner *et al.* 2004), they were excluded from these calculations. Runs during which ants were consuming plant secretions without returning any solid food item were classified as unsuccessful, since the uptake of liquid food could not be quantified (see above).

By combining the survival rate, the foraging effort, and the foraging efficiency of individual ants, the daily foraging success rate of the entire colony (S_c) could be recalculated indirectly (see *Colony activities*):

$$S_c = \frac{\sum_{i=1}^{\infty} S_i \cdot e^{-\mu(i-1)} \cdot R_i}{\sum_{i=1}^{\infty} e^{-\mu(i-1)} \cdot R_i} \qquad (4)$$

where S_i is the individual foraging efficiency on Day i, μ is the daily mortality rate, and R_i is the number of foraging runs per ant on Day i.

Sector fidelity (the degree to which an individual ant remained faithful to a particular foraging direction), was expressed as the directionality r ($0 \leq r \leq 1$) of the outbound runs. According to circular statistics (Batschelet 1981) a value of $r = 0$ means that the outbound runs of a particular ant were distributed evenly over all 30°-sectors mentioned above (that is, the ant did not show any sector fidelity); a value of $r = 1$ indicates that the ant always left the nest by crossing the recording circle within the same 30° sector (maximum sector fidelity).

Occasionally, individually marked ants were lost while being tracked or missed when leaving or entering the nest. This happened especially during periods of high activity. Therefore, and due to the highly variable life spans of the ants, sample sizes varied between different test series. The sample sizes used for graphical and numerical analyses are indicated in the respective figures and/or the corresponding text.

Results

General foraging characteristics

Foraging efficiency and type of food

The foraging success rates were surprisingly low. They reached 0.17 at Nest 3, 0.06 at Nest 9, and 0.15 at Nest 10. Foragers of Nest 9 returned 926 mg solid food during two consecutive days. In all, 87 of the 107 collected items weighed less than 10 mg, and only 11 items were heavier than 20 mg (range: <1–65 mg). The body weight of successful foragers varied between 7 mg and 22 mg. Ant weight and food weight did not correlate ($r = +0.0259$, $n = 107$, $P = 0.7915$). For the most part, ants returned insect carcasses (83.1%), predominantly hymenopterans (Fig. 1). Plant material, primarily seeds, was collected only rarely (6.6%).

#### Diurnal activity patterns and temperature dependencies

Foraging started when the soil surface temperatures approached 50°C (Fig. 2). In mid-February, the foraging

activity extended over 6–8 h with 1000–1500 foraging runs per day and colony. In mid-March, foraging was delayed. The duration of the above-ground activity was markedly reduced, although soil surface temperatures were similar to (Fig. 2*b*), or only slightly lower than (Fig. 2*a*) during the peak season. However, on cloudy days the soil surface temperatures were markedly lower. As a consequence, above-ground activities were shorter, and colony foraging efforts were lower (Fig. 2*c*). Ants generally stopped foraging and blocked the nest entrances as soon as it started to rain.

The activity patterns differed between nests and seasons. During the peak season Nest 3 performed most foraging runs in the morning (Fig. 2*a*). At ~1030 hours foraging activity dropped markedly and was resumed 2 h later. At Nest 10, on the other hand, foraging activity was characterised by alternating periods of high activity (bursts) and low activity (breaks), but there was no extended break around 1200 hours (Fig. 2*b*). During the late season the rate of outbound runs was low but constant right from the onset of foraging. Foraging activity levelled off after 2–3 h and did not exceed 350 runs per day and colony.

Forager force and mortality

The survival curve (Eqn 1) fitted to the data of individually marked ants of Nest 3 suggests a daily mortality rate of 0.206 ± 0.009 ($\mu \pm$ s.e.) (Fig. 3), and hence, a daily loss of ~18.6% ($1 - e^{-\mu}$). This results in a relatively short foraging half-lifetime of 3.4 days (Eqn 2), a life expectancy of 4.9 days (μ^{-1}), and a forager force of ~107 ants per day during the peak season (Eqn 3). The longest-lived ant from the daily cohorts was seen until 23 days after marking. Another ant from a previous experiment at the same nest (Nest 3) was still foraging 27 days after marking (foraging age at the time of marking unknown).
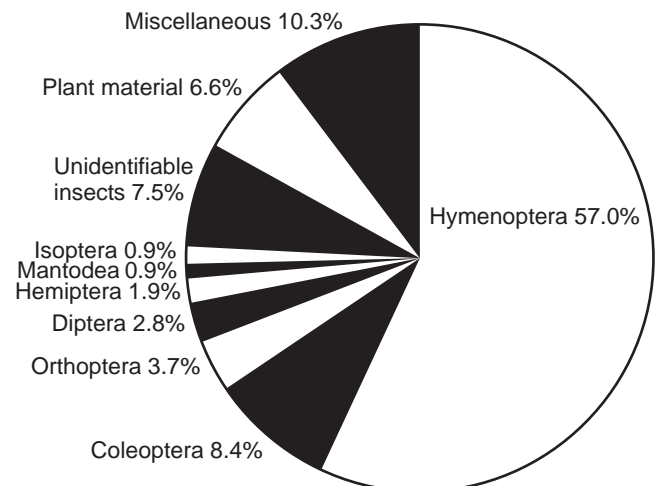
Fig. 1. Composition of the diet of *M. bagoti*. Shown are the relative frequencies of different categories of food items ($n = 107$) as identified on 23 and 24 February 2003 at Nest 9.

Four of the individually marked ants were still alive at the end of the recording period. Of the remaining 16 foragers, one was killed by workers of an *Iridomyrmex* species, four were killed by small paralysing spiders of the family Zodariidae, and another nine were not observed returning from their last foraging excursions (trajectories not recorded). Hence, only two ants (10%) of the sample of recorded foragers seem to have died inside the nest, since they were not resighted until the end of the experiment (i.e. for one and two weeks, respectively).

Does recruitment occur?

No foragers recruited nest mates to the feeder (Fig. 4). Fifteen minutes after the installation of the food source, four workers were shuttling back and forth between the nest and the feeder. This caused an increase in the number of out-

bound runs that was rather unspecific in terms of direction-ality. Between 1015 and 1115 hours the rate of foragers dis-covering the feeder remained constant at ~0.7 ants per minute, suggesting random finding (recruitment would be indicated by an exponential increase of new ants at the feeder). The rate of arrival levelled off thereafter, most likely because of the colony's limited pool of potential foragers. At the end of the 2-h test period 59 foragers had detected the artificial food source. The outbound activity dropped within 2 min after the removal of the feeder (Fig. 4).

The higher number of ants leaving the nest within the feeder sector, compared with the remaining sector (Fig. 4), was for the most part due to the much shorter round-trip times of foragers exploiting the feeder (1–2 min) than of nat-urally foraging ants (on average ~12 min; see Fig. 6). A rough calculation supports this view. The ratio of the
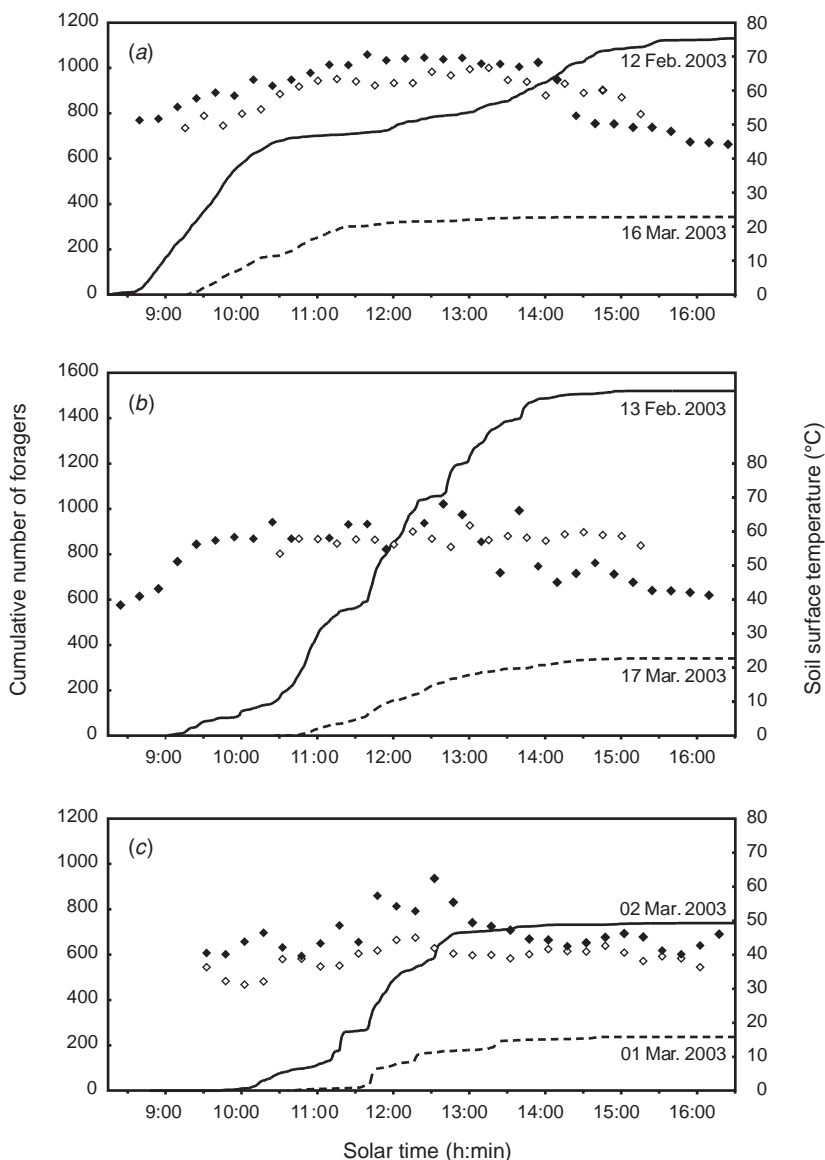
Fig. 2. Diurnal activity patterns. Shown are the cumulative numbers of ants leaving the nest (lines, left ordinate), and the soil surface temperatures measured in the sun (diamonds, right ordinate). Foraging activity was measured at (*a*) Nest 3 and (*b*) Nest 10 during the peak season (solid lines, closed diamonds), and during the late season (broken lines, open diamonds). (*c*) Foraging activity was measured on cloudy days at Nests 4 (broken line, open diamonds) and 11 (solid line, closed diamonds).
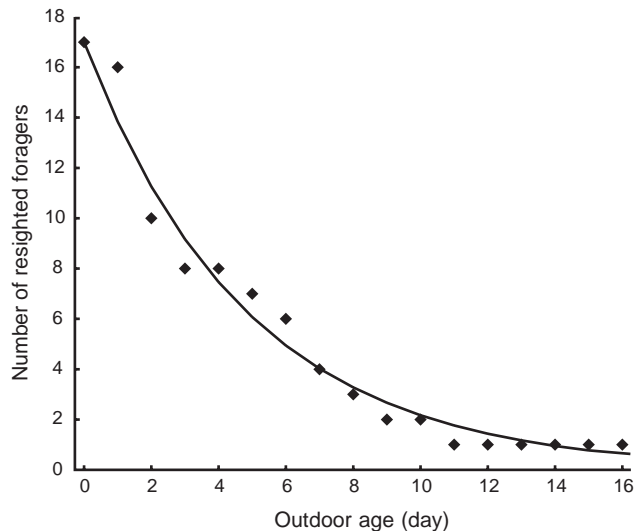
Fig. 3. Survival curve of individually marked foragers. One ant lived for more than 16 days. Three ants were only 1–4 days old at the end of the experiment, because they were marked late in the recording period (see Methods), and another five ants were never seen foraging. They were excluded from the analyses. Outdoor age '0 days' corresponds to outdoor activity 'Day 1' in Figs 5–9.

angular widths of the feeder sector to the remaining sector (1:3) was counteracted by a ratio of ~1:10 for the round-trip times of foragers leaving the nest through one or the other sector. This resulted in a 3–4 times higher number of ants leaving the nest through the feeder sector (Fig. 4).

Ontogeny of foraging behaviour

Five of the individually marked ants were never seen foraging. This was unlikely to be due to the marking procedure because four of them were resighted at the nest entrance, two of them a week after marking. The remaining 20 ants (80%) started above-ground activity with a delay of 1–4 days after marking. This delay was probably due to a slow onset of

foraging activity, since experienced foragers usually resumed foraging immediately after marking (observation made during the recruitment experiment).

In total, 5–10 of the individually marked ants were foraging on each day during the recording period. Foragers usually started their above-ground activities with a few (maximum seven) exploration runs (see Fig. 8a). These runs were relatively short (maximum path length: 19.6 m), and in most cases they lasted less than 1 min (maximum duration: 3 min).

In addition to the exploration runs, foragers performed, on average, one foraging run on the first day of their outdoor lives (1.1 ± 0.3 runs, mean $\pm$ s.e.). With increasing foraging experience the number of runs per day gradually increased (Fig. 5). The relationship between the cumulative number of foraging runs (N_d) and the ants' foraging experience, as measured in terms of days of outdoor activity (d), can be described by a power function (Fig. 5). The longest-lived individually marked ant (YB; see Fig. 9) performed 86 foraging runs within the first 16 days of its outdoor life (N_{16} predicted by the power model: 90 runs).

With increasing foraging experience the lengths and durations of the runs gradually increased from 44.0 ± 8.3 m and 6.9 ± 1.1 min (mean $\pm$ s.e.) on the first two days to 118.2 ± 35.8 m and 16.5 ± 1.7 min after seven days (Fig. 6). The longest run recorded had a path length of 283.2 m. The maximum duration of the runs was 64 min (trajectory not recorded). The average maximum foraging distance per ant was 20.3 ± 3.1 m (mean $\pm$ s.e., $n = 15$ ants). However, 90% of the runs were confined to distances of <20 m from the nest entrance (135 runs of 15 ants), with an average maximum ant-nest distance of 10.6 ± 1.3 m (mean $\pm$ s.e., $n = 15$ ants). Only two ants were foraging at distances >30 m (maximum distance observed: 42.9 m).

The ants exhibited sector fidelities that were amazingly high right from the beginning of their foraging lives (Fig. 7a). Nevertheless, long-lived ants further increased
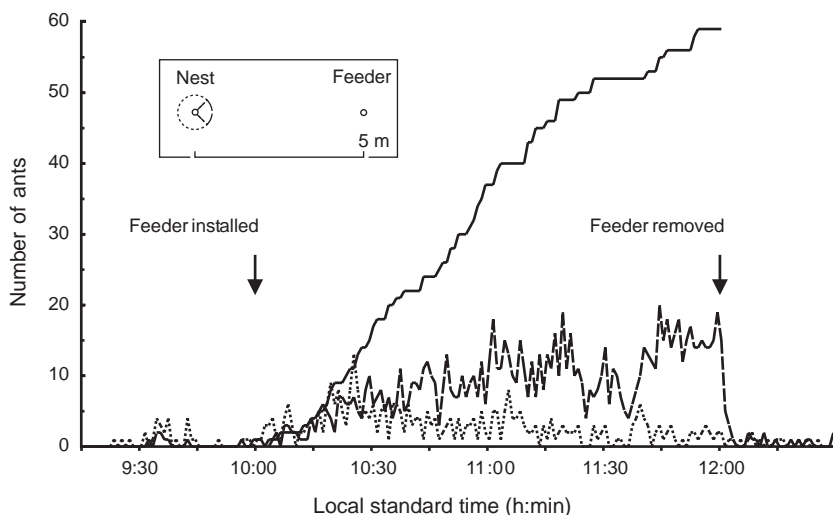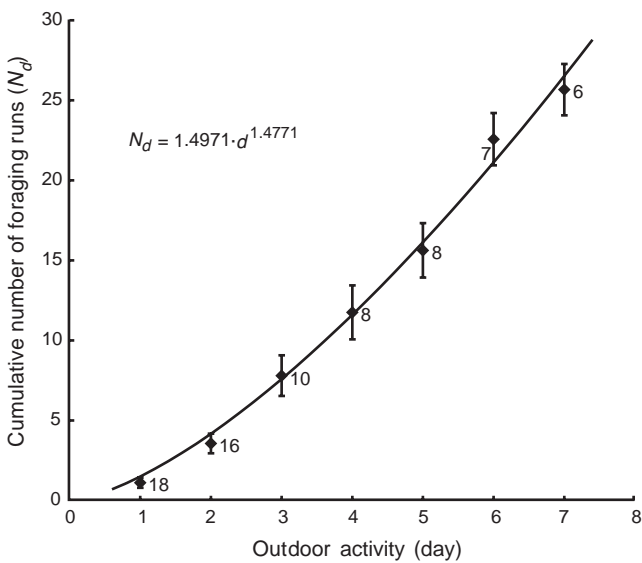

Fig. 4. Recruitment experiment. Shown are the cumulative numbers of new ants arriving at the feeder (solid line), and the numbers of outbound ants per sector and minute (broken line, feeder sector; dotted line, non-feeder sector; see inset). The feeder was installed between 1000 and 1200 hours (arrows).

their faithfulness to a particular foraging direction with increasing foraging experience. For example, ant BS (Fig. 8) found its first food item during Run 7 on Day 4. Although it refused to carry the food item to the nest, it did not change its foraging direction thereafter. Ant YB (Fig. 9) limited its relatively broad foraging sector of the first week to a particular direction on Day 8. From Run 30 onwards it kept visiting the same area under a river red gum, *Eucalyptus camaldulensis*, where it regularly consumed plant secretions.

Unlike the ants' sector fidelity the average individual success rates increased steadily (Fig. 7*b*). Neglecting liquid feeding, the success rate of ant YB (Fig. 9), for example, increased gradually from 0.05 (Runs 1–20) to 0.20 (Runs 21–40), 0.45 (Runs 41–60) and 0.54 (Runs 61–86). Including the uptake of liquids, the success rate of this ant was markedly higher. However, only 5 of the other 19 individually marked foragers were observed consuming liquids, one ant during two runs, and two ants each during one and four runs, respectively.

Among individual ants the foraging efficiencies varied substantially. Eight short-lived foragers (1–8 foraging runs performed during 1–5 foraging days) did not retrieve anything at all. Ant YB, the most successful ant in terms of the number of food items retrieved (28), was unsuccessful until its Run 15 performed on Day 5 (Fig. 9). The most successful ant in terms of success rate (0.67) performed two exploration runs on the first day, followed by an unsuccessful and a successful foraging run on Day 2, and two unsuccessful and four successful runs on Day 3.

Having estimated the average survival rate (Fig. 3), the foraging effort (Fig. 5), and the foraging efficiency (Fig. 7*b*) of individual ants at Nest 3, the daily foraging success rate of the colony (Eqn 4) can be predicted to be ~0.23. This estimate is somewhat higher than the one derived directly from monitoring the entire forager force during one full day (efficiency: 0.17). This indicates that, in the latter case, a few runs had been misclassified, probably because some ants were returning from exploration runs or nest-cleaning activities (see Methods). During periods of high activity it was impossible to distinguish such activities from foraging.

Discussion

We investigated individual as well as collective components of the foraging ecology of the Australian desert ant, *M. bagoti*. The interior colony dynamics of this species are still unknown, but workers appear at the nest entrance 1–4 days before they shift from interior to exterior duties. Once they started foraging they usually do so daily.

Forager life history and intraspecific competition

An ant's outdoor activity typically starts with a few exploration runs, and, on average, with one foraging run on the first day of its outdoor life. The foraging effort then gradually increases with age (Figs 5, 6). However, due to the high daily mortality (Fig. 3) and the low initial foraging efficiency (Fig. 7*b*) only half of the foragers are successful more than once during their lives. This suggests that a colony's nutrient supply is, for the most part, provided by a relatively small fraction of long-lived foragers, which become increasingly efficient in collecting food. Yet this higher efficiency can be

Fig. 5. Foraging effort. Shown are the cumulative numbers of foraging runs performed by individual ants (mean ± s.e.) as a function of foraging experience. The numbers next to the diamonds represent the numbers of individually marked ants foraging on the respective day. The power function is fitted through daily mean values ($R^2 = 0.99$), which are calculated from average values per ant.
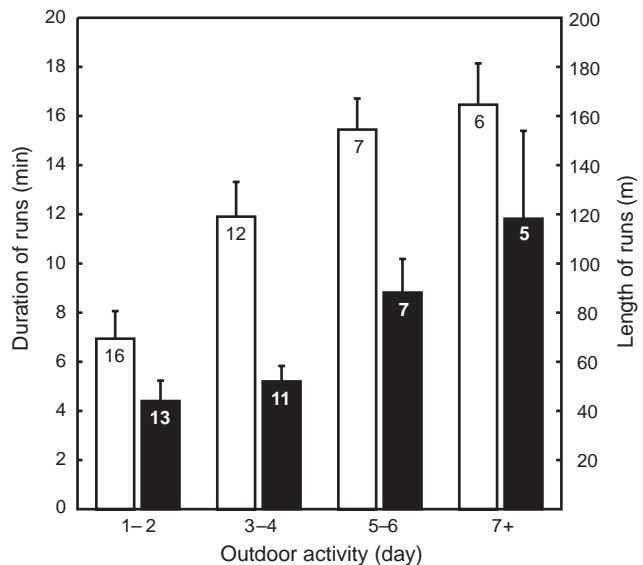
$$N_d = 1.4971 \cdot d^{1.4771}$$

Fig. 6. Duration (white bars, left ordinate) and path length (black bars, right ordinate) of foraging runs. The numbers inside the bars represent the numbers of individually marked ants foraging on the respective day. Means are calculated from average values per ant.

explained only partly by increasing site fidelity (that is, familiarity) since the success rate grows gradually, whereas the sector fidelity is high from the beginning and does not increase until Day 5 (Fig. 7). Hence, foraging success may be the cause for site fidelity rather than the consequence of it (Wehner *et al*. 2004). Nevertheless, the average foraging success is strikingly low. This suggests a low food density relative to the nest (or forager) density, and hence, intense competition among *M. bagoti* colonies. This conclusion is supported by two observations.

First, foraging ranges of adjacent colonies largely overlap (maximum foraging distance: >20 m; nearest-neighbour distance: 20 m). Consequently, *M. bagoti* seems to maximise the inter-colony distances (nests tend to be overdispersed; see Methods), and, hence, to optimise the exploitation of its foraging area. Accordingly, the average foraging distance (10.6 m) is about half of the nearest-neighbour distance. As is the case for various *Cataglyphis* species (Wehner *et al*. 1983; Dillier and Wehner 2004), 90% of all foraging runs of *M. bagoti* are confined to a circle with a radius equal to the mean nearest-neighbour distance.

Second, battles among nearby colonies are fairly common. During these fights workers of one colony collectively attack members of an adjacent colony at their nesting site. This is in contrast to a congener of the *M. aeneovirens* (Lowne) species-group in the monsoonal tropics. In this species inter-colony aggression seems not to occur (Hoffmann 1998). While the average foraging distances of *M. aeneovirens* (9 m) are similar to those of *M. bagoti*, the inter-colony distances are about twice as high in the former species (42.8 m), and the inter-colony competition seems to be low (Hoffmann 1998). Accordingly, average colony foraging efficiency is much higher in *M. aeneovirens* (0.51) than it is in *M. bagoti* (0.06–0.17).

Because of the spatial unpredictability of the food items (dead insects: Fig. 1) within a nutritionally poor environment, *M. bagoti* might be expected to develop techniques for rapidly exploiting occasionally abundant food sources (Carroll and Janzen 1973). However, the sudden appearance of such a food source might be fairly rare within the foraging range of a colony. This is in accord with the fact that efficient recruitment behaviour (e.g. pheromone laying or tandem running: Carroll and Janzen 1973) was not observed (Fig. 4).

Interspecific competition and predation

Foragers of *M. bagoti* are active during the hottest hours of day and year (Fig. 2). This probably relaxes interspecific competition as well as predation from less heat tolerant species (see Briese and Macauley 1980; Wehner *et al*. 1992). In fact, the extreme thermotolerance of *M. bagoti* (Christian and Morton 1992) could be the main ecological reason why this species can coexist in large numbers with the highly aggressive *Iridomyrmex* ants, which are known to suppress

other species of ants (Andersen and Patel 1994; Hoffmann 1998; Shattuck and Barnett 2001). While *M. bagoti* forages at its thermal physiological limit (Christian and Morton 1992), *Iridomyrmex* ants generally avoid exposure to full sun and retreat to cooler places. However, occasionally an unwary *M. bagoti* forager might still fall prey to *Iridomyrmex* ants (see Results) which kill and consume any other ant species they accidentally encounter.

An important predator of *M. bagoti* at the study site is a small hunting spider of the family Zodariidae. This spider is usually found in the leaf litter from where it stalks individual
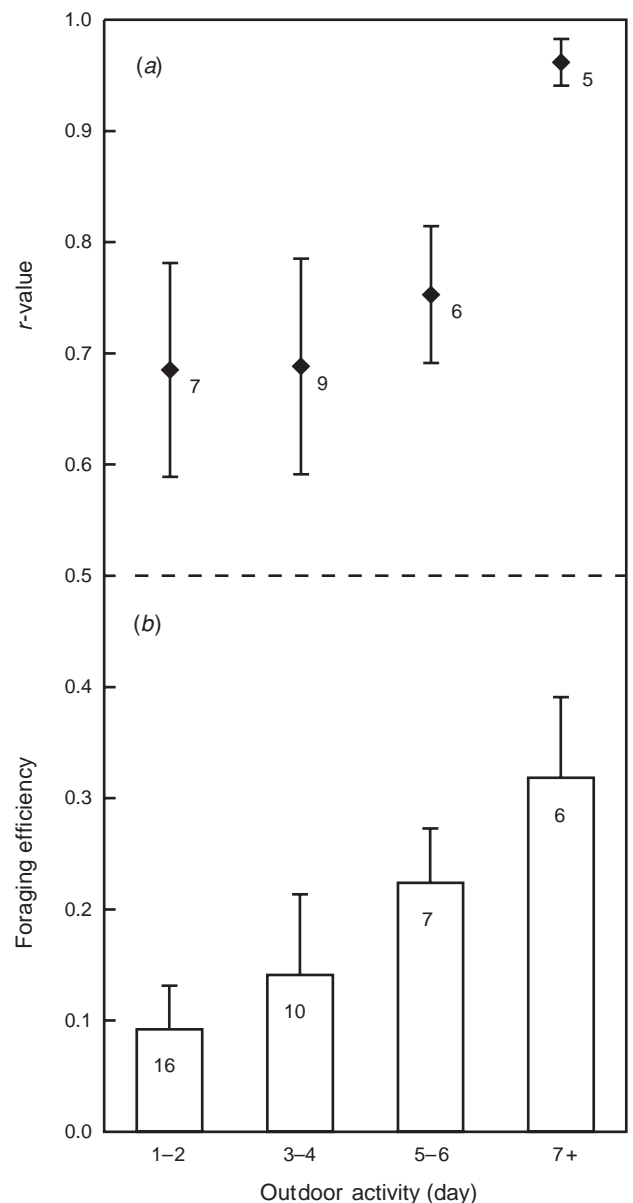
Fig. 7. The progression of (*a*) sector fidelity and (*b*) foraging efficiency of individual ants. Numbers represent the number of individually marked ants foraging on the respective day. Means are calculated from average values per ant.

ants. It strikes an ant with a single bite and then retreats into the leaf litter and waits until the ant is paralysed (see also Harkness and Wehner (1977) for *Cataglyphis*). Other potential predators at the study site include the many insectivorous birds and lizards. However, these animals were timid and never directly observed preying upon *M. bagoti* or any other ant species.

How does M. bagoti *compare to* C. bicolor*?*

M. bagoti and *C. bicolor* live in ecologically similar habitats (low-shrub semi-deserts). They are of comparable size (10–50 mg: Schmid-Hempel 1983; Christian and Morton 1992), and they collect the same type of food (dead arthropods) by using the same mode of foraging ('diffuse foraging': Traniello 1989). Yet, with a few exceptions, only the most experienced *M. bagoti* foragers reach foraging efficiencies as high as those usually observed in *C. bicolor* (Table 1). A direct comparison between species-specific traits of *M. bagoti* and *C. bicolor* might reveal a few explanations for the strikingly different success rates of the two species.

First, the inter-nest (i.e. nearest-neighbour) distances, the nest densities, and the forager forces are similar for *M. bagoti* and *C. bicolor* (Table 1). This implies that the forager densities are roughly the same in both species. However, due to the polydomous colony structure of the latter species, average distances between colonies are larger in *C. bicolor*, and hence, inter-colony competition is probably lower. This might partly explain the larger foraging ranges of *C. bicolor*

(Table 1) and consequently account for the longer foraging runs of this species compared with those of *M. bagoti*. Hence, during a single foraging run *C. bicolor* searches for a longer period and in a larger area than does *M. bagoti*, and thereby is likely to increase its success rate.

Second, a colony's foraging efficiency is the result of the foraging activities of individual ants. Thus, it reflects individual life-history parameters such as success rate, foraging effort and forager mortality rate (see Eqn 4). Since in *C. bicolor* the initial individual foraging success is more than twice as high as it is in *M. bagoti* (Table 1), the higher average foraging efficiency of *C. bicolor* than of *M. bagoti* is just a consequence of the higher initial foraging effort (that is, the higher number of runs performed per ant and per day) and the higher life expectancy of the former species.

Further, it should be noted that the methods used for assessing the efficiencies of *M. bagoti* and *C. bicolor* foragers underestimated the true success rates, since runs for liquid feeding were counted as unsuccessful. Although honeydew and plant exudates have been hypothesised to play an important role for ant productivity in arid Australia, they do so mostly for behaviourally dominant ants (e.g. *Iridomyrmex*: Andersen 2003). Nevertheless, the contribution of liquids to the nutrient supply of *M. bagoti* might still be substantial, as indicated by the 'living honey pots' (Conway 1992). On the other hand, liquid food is of minor importance for *C. bicolor* (Schmid-Hempel 1983). Hence, including liquids into the assessment of foraging success might considerably reduce the difference between the two species.
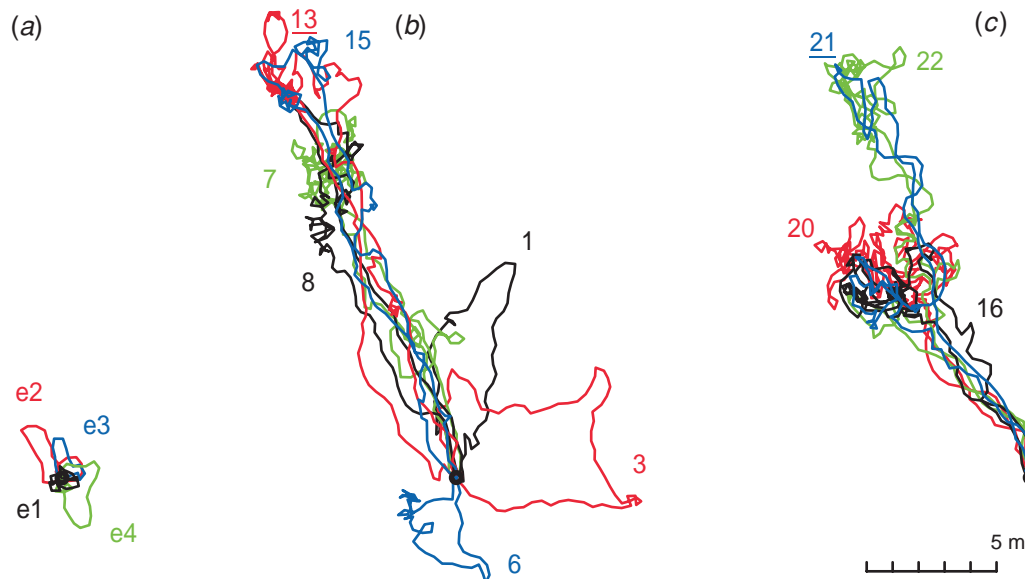
Fig. 8. Spatial layout of runs performed by ant BS. (*a*) Exploration runs e1 to e3 were performed during the first 2 days of the ant's outdoor life. Run e4 was the first run on Day 4 and was performed after the first two foraging runs. (*b,c*) Ant BS completed 22 foraging runs within 7 days. During Run 7 it refused a potential food item, but stuck to the same foraging direction thereafter. Underlined numbers indicate the locations where it had found a food item. It was successful on Runs 9 (trajectory not recorded), 13, 17 (trajectory not recorded) and 21. Ant BS did not return from foraging Run 23 (trajectory not recorded). The small circle indicates the nest entrance.
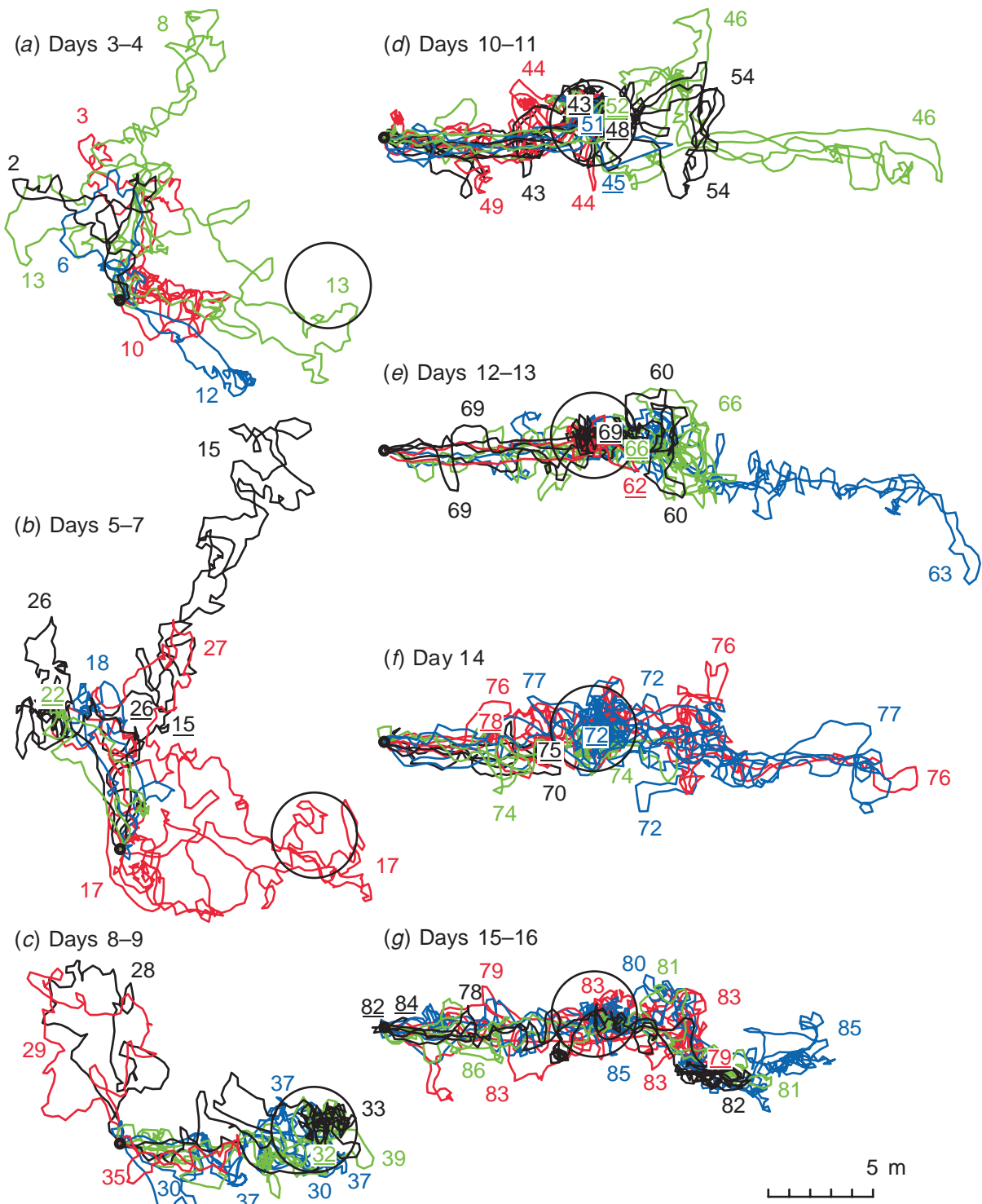
Fig. 9. Spatial layout of foraging runs performed by ant YB. Run 1 was performed on Day 2 after three exploration runs (one on Day 1 and two on Day 2; trajectories not recorded). Ant YB kept foraging in a relatively broad sector until Run 30 on Day 8. Thereafter, it regularly visited a specific area (indicated by the circle) where it consumed plant secretions. Uptake of liquid food was observed during Runs 33, 35, 37, 39, 43, 44, 46, 48, 49, 51, 52, 54, 60, 62, 63, 66, 72, 74, 76 and 77. Ant YB returned 28 solid food items (Runs 15, 22, 25, 26, 32, 43, 45, 48, 50, 51, 53, 56, 57, 58, 61, 62, 64, 66, 68, 69, 71, 72, 73, 75, 79, 80, 82, 84). Underlined numbers indicate the locations where ant YB had found a food item. It was not seen foraging for 3 days after Run 86 on Day 16 (trajectory not recorded), but resumed foraging thereafter. The small circle indicates the nest entrance.

Table 1. Colony characteristics and foraging parameters of two desert ant species

M. bagoti and *C. bicolor* inhabit the low-shrub and grassland deserts of central Australia, and the low-shrub semi-deserts of northern Africa, respectively. Both species are diurnal scavengers, characterised by an individual mode of foraging. Parameter estimates were obtained during the ants' main activity period (*M. bagoti*, January–March; *C. bicolor*, June–August); they are given as means or ranges of observed values. If not mentioned otherwise, values for *M. bagoti* refer to the present study

	M. bagoti	*C. bicolor*
Colony structure	Monodomous(?)	Polydomous (max. 11 nests per colony)[A,B,C,D]
Density (per hectare)	Nests: 13	Colonies: 2.6–6.6[A,D]
		Nests: 9.9–22.0[A,B,D]
Spatial distribution	Nests: overdispersed	Colonies: overdispersed[D]
		Nests: aggregated[D]
Nearest neighbour distance	Nests: 20.0 m	Colonies: 29.0–45.7 m[B,D]
		Nests: 8.5–18.2 m[D,E]
Forager force per nest	107	93[A,E]; 290[C]; 20–600[B]
Life expectancy	4.9 days	6.0–6.5 days[A,C,F]
Mean foraging distance (maximum)	10.6 m (42.9 m); 12.0 m[G]	39.9 m (87.0 m)[E]
Average run duration	<20 min	>20 min[C]; 53–54 min[A,B]
Daily foraging effort per ant	Gradually increasing: 1 run on Day 1, 5 runs on Day 6	Constant: 3–4.2 runs per day[A,B,D,F]
Initial individual foraging efficiency	<0.10	≥0.25[C,F]
Average foraging efficiency	0.06–0.23	0.40–0.53[A,B,E,F]

[A]Wehner *et al.* (1983). [B]Schmid-Hempel (1983). [C]Schmid-Hempel and Schmid-Hempel (1984). [D]Dillier and Wehner (2004). [E]Wehner (1987). [F]Wehner *et al.* (2004). [G]Kohler and Wehner (2005).

Finally, the foraging efficiencies of individually searching ants are largely determined by the distribution and the density of potential food items. For thermophilic scavengers food availability is a combination of items not taken by other species and items that become available during the hottest periods of the day. Because ant biomass in arid Australia is much higher than in northern Africa (Andersen 2003), the lower foraging efficiency of *M. bagoti* than of *C. bicolor* might also be due to stronger competition of the former species with non-thermophilic ants.

Acknowledgments

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