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Search strategies of ants in landmark-rich habitats

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Abstract Search is an important tool in an ant's navigational toolbox to relocate food sources and find the inconspicuous nest entrance. In habitats where landmark information is sparse, homing ants travel their entire home vector before searching systematically with ever increasing loops. Search strategies have not been previously investigated in ants that inhabit landmark-rich habitats where they typically establish stereotypical routes. Here we examine the search strategy in one such ant, *Melophorus bagoti*, by confining their foraging in one-dimensional channels to determine if their search pattern changes with experience, location of distant cues and altered distance on the homebound journey. Irrespective of conditions, we found ants exhibit a progressive search that drifted towards the fictive nest and beyond. Segments moving away from the start of the homeward journey were longer than segments heading back towards the start. The right tail distribution of segment lengths was well fitted by a power function, but slopes less than -3 on a log-log plot indicate that the process cannot be characterized as Lévy searches that have optimal slopes near -2. A double exponential function fits the distribution of segment lengths better, supporting another theoretically optimal search pattern, the composite Brownian walk.

Keywords Search · Navigation · Ants · Composite Brownian walk · Lévy walk

Introduction

Search strategies in central place foragers, such as ants can be studied in two distinct scenarios, search for food and search for the nest entrance at the end of a foraging bout. Foraging ants revisit food rich sites regularly (Kohler and Wehner 2005). The duration of the search when re-locating the site changes with the quality of the food, a carbohydrate-triggered search lasts longer than a protein-triggered search (Fourcassié and Traniello 1994), but is not affected by experience (Fourcassié and Traniello 1993). While homing, desert ants take the shortest way to reach the vicinity of the nest by integrating distance and directional information acquired during their foraging trip (Collett and Collett 2000; Wehner 1982; Wehner and Srinivasan 2003). This behaviour called path integration accumulates both systematic and random errors (Merkle et al. 2006; Müller and Wehner 1988). Thus after the path-integrated vector is executed, foragers must employ a search strategy to find the inconspicuous nest entrance.

Arthropods are known to search systematically for their burrow/nest with search loops that gradually increase in size, with the start and the end of each loop located at the same point (Hoffman 1983; Müller and Wehner 1994; Wehner and Srinivasan 1981). This is considered an optimal strategy, as search is concentrated in the area where the

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target is most likely to be present. Desert ants of the genus *Cataglyphis* use such a search strategy in their saltpan habitat where the available landmark information is sparse. While homing, these ants execute a path-integrated home vector followed by a near-optimal looping search (Müller and Wehner 1994).

Navigation behaviours of ants in cluttered habitats, such as the Central Australian desert ant *Melophorus bagoti*, are quite different from those in the featureless saltpan habitats. *M. bagoti* establishes idiosyncratic routes when foraging in familiar terrain and relies on its path integrator only in the absence of familiar route cues (Kohler and Wehner 2005; Narendra 2007a; Sommer et al. 2008; Wehner et al. 2006). In using the path integrator after being displaced to unfamiliar terrain, these ants travel on average only half the homeward distance (Narendra 2007a) and then rely on distant landmarks to locate the nest (Narendra 2007b). Interestingly, when they are restricted to foraging in channels that block distant landmark information and render the outbound and homebound environments very similar, the ants travel the entire homeward distance (Narendra 2007a).

While homing in a featureless saltpan habitat, ants have only one target to find, the nest, thus rendering the target density very low. In following the established routes in a cluttered environment, the target density is potentially much higher as various features may serve as land and route marks. Once an ant has found its familiar route, it adheres to this route to reach home (Kohler and Wehner 2005; Narendra 2007b; Sommer et al. 2008; Wehner et al. 2006). Search strategies required in such a habitat might, hence, be different from those in a featureless habitat. Here we examine the search behaviour of the ant *M. bagoti*, as they search for the nest in one-dimensional channels.

Detailed search behaviour has been recently examined in a number of animals, and at least two proposals for optimal search patterns have been raised. One theoretical optimal pattern is the Lévy flight or walk, which we will call Lévy search (Sims et al. 2008; Viswanathan et al. 1999). Lévy searches are specialised search patterns that comprise of clusters of short segment lengths, interpolated by rarer longer segment lengths, which themselves are interpolated by even rarer, even longer segment lengths. These searches result in fractal (scale-free) movement trajectories, and are considered an optimal strategy to locate targets of low density (Viswanathan et al. 1999). To detect a Lévy search, the behaviour is categorised into search segments, and the distribution of the lengths of search segments is examined. Both segment length (*x* axis) and frequency (*y* axis) are plotted on log scales. A Lévy search is indicated by a linear function fitting the right tail of the distribution with a slope between −1 and −3, with −2 being optimal (Sims et al. 2008; Viswanathan et al. 1999). A linear fit is indicative of a power function relating frequency to search-segment

length. The function is said to indicate scale-free search because at any scale, the same power law characterises the search distribution.

Lévy searches have been found in several biological systems including sharks, bony fishes, sea turtles, penguins (Sims et al. 2008), and spider monkeys (Ramos-Fernández et al. 2004). Since Lévy walks appear as patterns exhibited by an animal searching for patchily distributed food, most studies have investigated the presence of these walks only while animals are foraging. To the best of our knowledge, only one study has explored the possibility of animals using these scale-free searches while homing (Reynolds et al. 2007). Using harmonic radars on honeybees, Reynolds et al. (2007) argue that homing bees that have not found the hive during a systematic search switch to a Lévy-flight search wherein they do not return to the origin of the search at the end of every loop.

The topic of Lévy searches remains controversial (Benhamou 2007; Edwards et al. 2007; Plank and James 2008; Sims et al. 2007) and methods of data analysis are important for correct identification of Lévy searches (Benhamou 2007; Sims et al. 2007). Recently, Benhamou (2007) used computer simulations to identify another efficient search strategy, the composite Brownian walk. The strategy consists of a mixture of two exponential distributions of search-segment lengths. The two distributions differ in mean length. One exponential distribution has a short mean length, thought to reflect intra-patch searching; the other has a much longer mean length, thought to reflect inter-patch searching. To detect the exponential function, the *y*-axis (frequency) is plotted on a log scale while the *x*-axis (search-segment length) is plotted on a linear scale.

In this paper, we examine the search strategies used by *M. bagoti* ants as they search for their nest. To collect many search segments, we confined the ants to a one-dimensional environment of channels. We examined the characteristics of the search strategy used by ants to locate their nest. We then plotted the distribution of search-segment lengths in both log-log and log-linear fashion to identify if the search has characteristics of a Lévy walk or a composite Brownian walk.

Materials and methods

Study area and study species

We studied the thermophilic ant, *Melophorus bagoti* Lubbock, which inhabits the semi-arid desert habitat in central Australia (Fig. 1). These ants construct nests in sandy clayey loamy soil, where the ground cover is dominated by Buffel grass (*Cenchrus ciliaris*) and the overstory by tree species of *Acacia estrophiolata* and *Hakea eyreana*. The

Fig. 1 The major and median worker caste of the desert ant, *Melophorus bagoti* that inhabits the semi-arid deserts of Central Australia. Photo credit Ajay Narendra

study was carried out at Alice Springs, NT, Australia. *M. bagoti* are solitary foraging ants that begin foraging when soil surface temperature approaches 50°C (Christian and Morton 1992; Muser et al. 2005).

Experimental set up and general procedure

We trained ants to reach a feeder and return to the nest by travelling in channels (10 cm height and 10 cm width). We enclosed the nest from the side using a rectangular frame and provided two exits that led to two outward channels (6 m and 12 m length) and one entry point that led to a homeward channel. The channels were made of 1-m white plastic segments and were connected to each other to obtain the required length. The design allowed the ant to view 53° of the sky (in the transverse axis of the ant's visual field), if it walked in the centre of the channel. In the channel, the tussocks to the side would not be visible. A few trees were tall enough so that their top parts would be visible. A thin layer of sand was sprayed on the channel floor to provide friction. The training phase required ants to walk in the outbound channel (6 m or 12 m) and reach the feeder, where they were marked with coloured spots of acrylic paint on their gaster and mesosoma, for individual identification. The ants then had to return to the nest by travelling in the homeward channel that was placed parallel to the outward channels. Ants with different training regimes that returned to the feeder were captured individually in vials, transferred in the dark and released in the test channel. The test channel was 32 m in length and placed 10 cm away, parallel to the other channels. A measuring tape placed beside the test channel enabled the observer to read the turns taken by the ants, to the nearest 0.1 m. Here we recorded the search patterns exhibited by ants either for a 5-min period or till the ants reached the end of the test channel. Only search patterns of ants with food in their mandibles were recorded. To

qualify as a turn, an ant had to turn back and travel at least 20 cm, a measure used in previous studies (Cheng et al. 2006; Cheng and Wehner 2002; Narendra 2007a; Narendra et al. 2007a).

We tested if search patterns changed (1) with increase in experience, (2) when the distance travelled on the homeward journey was different from that of the foodward journey and (3) with the different locations of testing, providing different distant cues. To address the first question we captured ants that reached the feeder following different training trials: (a) naïve foragers, foragers that reached the feeder the first time, and (b) experienced foragers, foragers that were trained five times to the feeder. To address the second question, we trained one group of ants to reach the feeder by travelling 6 m and to return to the nest by travelling 12 m and conversely we trained another group of ants to reach the feeder by travelling 12 m to return to the nest by travelling 6 m, i.e., distance on the homeward journey was either reduced by half or doubled. Foragers that reached the feeder after five training trials were displaced from the feeder to a test channel, where their search pattern was recorded. Ants captured at the feeder were released in the test channel adjacent to the feeder location to ensure that the view the ants had outside the test channel was similar to that experienced on the homebound journey (Fig. 2a). The third question was whether distant cue information affected the search pattern of a homing ant. We hence moved the position of the test channel, such that, although it was parallel to the other channels, one end of the test channel was close to where the nest was located. Thus in this test situation, ants were released a long way (about 30 m) from the nest position, as compared to 6 or 12 m in the previous conditions (Fig. 2b). This experiment was carried out at a different nest and with ants from the 6 m group only and their search patterns were recorded after one, three and five training trials.

Analysis

We analysed the first 31 turns to describe the search patterns. We plotted the midpoints of successive turns, starting with the midpoint between Turn 1 and Turn 2, which corresponds to segment number 1 in the figures.

Distributions of search-segment lengths

We followed methods recommended by Sims et al. (2007), based on their simulations. A most important procedure is to bin data correctly. Our measurements were to the nearest 0.1 m, which means that the data were already in bins of segment lengths of the same linear size. Sims et al. (2007) recommended bins of the same log size. Accordingly, we pooled the data to make bins as close to 0.05 log units as
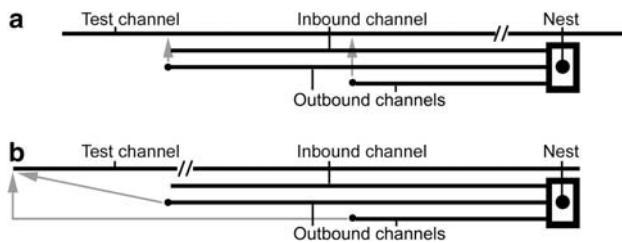
Fig. 2 Experimental set-up. Nest was enclosed from the sides by a *rectangular box*, which was connected to outbound channel of 6 and 12 m and to an inbound channel whose length was either 6 or 12 m. A feeder (*closed circle*) was placed at the end of outbound channels. Plastic gates between the channels and the nest enclosure provided control over entry and exit of the ants. Ants ready to test were captured at the feeder and released in the 32-m long test channel. The placement of the test channel and release points relative to the nest and feeder (*grey arrows*) differed in the experimental set ups (**a**) and (**b**). In (**a**), the release point was adjacent to the feeder location. In (**b**), the release point was beyond the feeder, ∼30 m from the nest

possible. The *x*-axis was measured as the geometric mean of the bins. With this log size, the first five bins at the short end are substantially (>30%) bigger than 0.05 log units even though they comprise only a single linearly sized bin. Sims et al. (2007) recommended adjusting the frequency according to the linear width of bins. In our case, this amounts to taking the average frequency across all the linearly sized bins pooled to make a log unit. We expressed frequencies in relative terms by dividing each frequency by the total number of segments. For this analysis, we pooled all the searches from all the conditions at each outbound distance. The frequency distributions were plotted for each outbound distance in both log-log and log-linear fashion.

Results

We begin by addressing the distance at which ants began their search in different conditions. For both 6 and 12 m groups, the distance at which ants began to search, with change in experience (6 m: naïve: 5.53 ± 2.54, $N = 20$; five trials: 7.13 ± 3.74, $N = 23$; 12 m: naïve: 12.19 ± 5.3; five trials: 12.39 ± 5.36), change in homebound distance (6 m shifted group: 8.81 ± 5.17, $N = 21$; 12 m shifted group: 10.6 ± 4.99; mean $\pm$ SD) and change in the point of release (6 m: one trial: 7.77 ± 4.4, $N = 17$; three trials: 7.82 ± 5.38, $N = 17$; five trials: 6.54 ± 2.86, $N = 15$; mean $\pm$ SD) did not differ for the respective outbound distances (6 m: $F_{5,107} = 1.4788$, $P = 0.202$; 12 m: $F_{2,56} = 0.666$, $P = 0.55$).

Search progression

The results from all conditions show a systematic progressive drift in the search, away from the starting point of the

run, with a larger drift in ants with 12 m outbound distance (Fig. 3). Both trained and naïve ants performed similarly (Fig. 3a). Different degrees of training given to ants from a different nest, along with a starting point far from the nest, led to similar results (Fig. 3b). The results were again similar, when on training trials the ants were displaced closer to the nest (12-m ants) or farther from the nest (6-m ants) before their return trips (Fig. 3c). The results for the 12-m ants that were displaced closer to the nest are especially interesting because the manipulation should, if anything, have reduced the tendency to drift forward in search.

Shown in Fig. 3a–c are the data averaged for different training regimes. Enormous individual variability is found in all conditions. In order to reduce the clutter in the figures, we have summarised the average standard deviation across segments in each condition along with the mean midpoint across segments (Fig. 3d). At each outbound distance, the search pattern is statistically similar. An analysis of variance between conditions and segments found neither a significant main effect of condition nor a significant condition by segment interaction. At each distance, the significant segment main effect was characterised by both a significant linear trend (12 m: $F_{1,551} = 623.84$, $P < 0.001$; 6 m: $F_{1,1508} = 452.83$, $P < 0.001$) and a significant quadratic trend (12 m: $F_{1,551} = 382.10$, $P < 0.001$; 6 m: $F_{1,1508} = 86.17$, $P < 0.001$).

Since results at each distance were similar across conditions, we pooled the data at each outbound distance from all the ants with at least 31 turns (Fig. 4a). The data are well fit by both a power function (in black) and a quadratic function (in grey) (Table 1). The power function contains a systematic pattern of errors in all the curves. The fit is too low for the first point, and then exceeds data points. The fit is better with a quadratic function, which has no notable systematic error, but contains one more free parameter. When a criterion for model selection was calculated, the Akaike information criterion (AIC), the quadratic function had lower (better) values (Table 1). For ants with 6 m outbound distance, we noted a downturn in the last few segments (Fig. 4a), and wondered if this was a continuing trend or a sampling error in the data. To test this, we examined the pattern for all 6-m ants that exhibited at least 41 turns (40 midpoints; Fig. 4b). The downturn did not continue, and again both a power function and a quadratic function provided good fits, with the AIC being better for the quadratic function (Table 1).

The lengths of the search segments, as a function of segment number are shown in Fig. 5. At each outbound distance, data from all conditions were pooled. At both outbound distances, the pattern of segment lengths was similar across conditions, with the analysis of variance finding neither a significant main effect of condition nor a significant interaction of condition by segment. Figure 5

Fig. 3 Midpoints of the first 31 search segments. **a** Search patterns of trained and naïve ants with outbound distance of 6 and 12 m (*n*'s, 6-m naïve: 4; 6-m 5-trial: 9; 12-m naïve: 6; 12-m 5-trial: 7). **b** Search patterns of ants with varying experience when release point was 30 m from the nest and not adjacent to the feeder (*n*'s, One-trial: 9; Three-trials: 11; Five-trials: 12). **c** Search patterns of ants trained to an outbound journey of 12 m and inbound journey of 6 m (12 m shifted, *n* = 9) and ants trained to an outward journey of 6 m and inbound journey of 12 m (6 m shifted, *n* = 13) before their search was recorded. **d** A summary of mean + SD of all different conditions. * Indicates conditions in which release points were ~30 m from the nest and were not adjacent to the feeder location
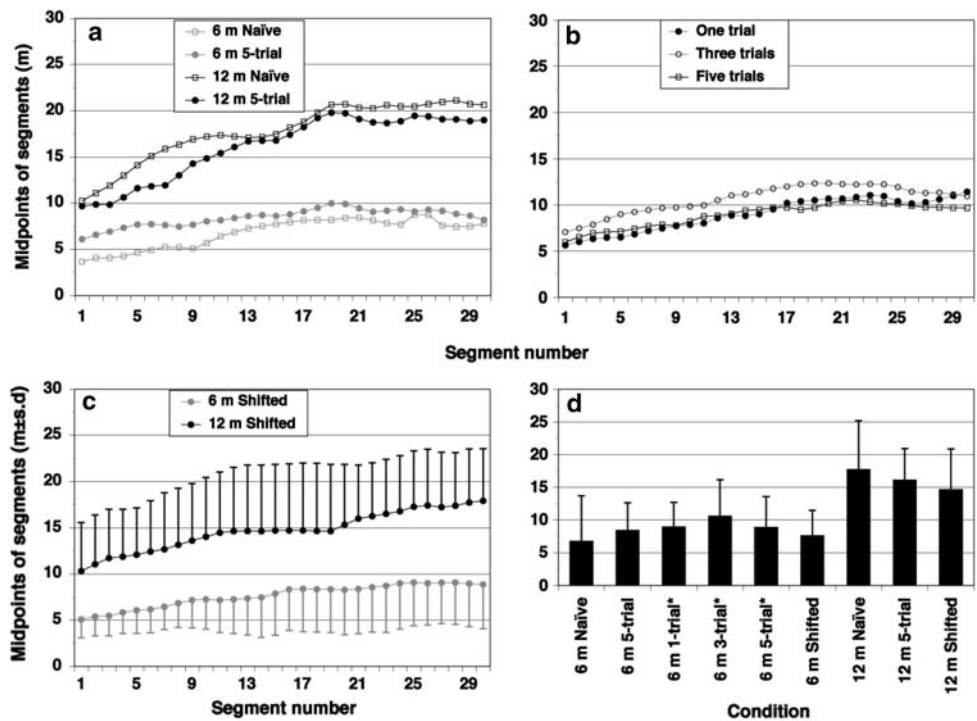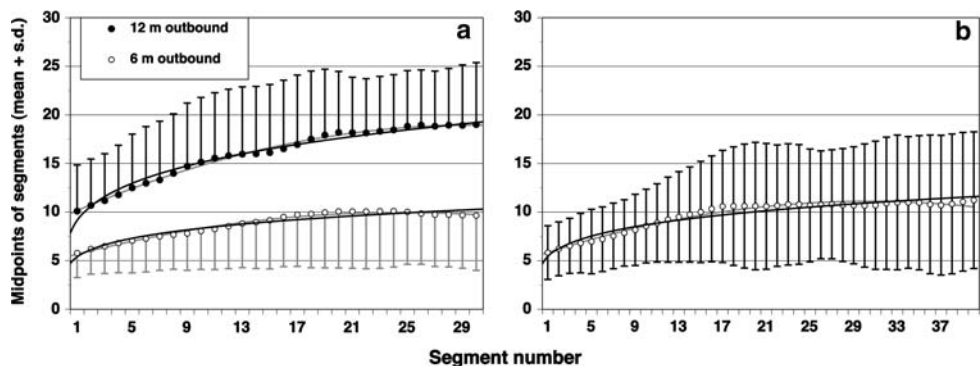

Fig. 4 Data pooled from all conditions to show midpoints of the search segments of ants with 6 and 12 m outbound distances. **a** Midpoints of the first 31 search segments at the two distances (*n*'s, 6-m: 58; 12-m: 22). **b** Midpoints of the first 41 search segments of ants from the 6 m outbound distance group (*n* = 29). Data are fitted with power (*black*) and quadratic (*grey*) functions

shows a see-saw pattern, with even segments (those heading away from the starting point of the run) longer than odd segments (those heading towards the starting point of the run); this holds for both outbound distances. The pattern is what we would expect if the search progresses farther and farther from the starting point of the journey (Fig. 4). Given the decelerating patterns found in Fig. 4, it is also not surprising that the amount of see-saw, that is, the difference in length between odd and even segments, diminishes with segment number. This pattern is especially evident for the 12-m ants that show a steeper rise than the 6-m ants at the start of the search. Best fitting straight lines revealed a small increase in segment lengths as the search progresses (Fig. 5). The linear trend is statistically significant in the 6-m ants ($F_{1,1508} = 23.58$, $P < 0.001$), but not in the 12-m ants ($F_{1,551} = 1.80$, $P = 0.180$). The lack of statistical significance in the latter trend might well be attributed to the large see-saws found in the beginning of the search. We thus examined only the lengths of the odd segments in 12-m ants. The linear trend in this case was statistically significant ($F_{1,266} = 28.04$, $P < 0.001$).

The amount of increase in segment length per turn is small, with similar slopes of increase in the two outbound distances (Fig. 5). The similarity is especially clear when only odd-numbered segments are considered, eliminating the distorting effects of the widely fluctuating even-segment lengths. Over 29 turns, the increase in segment length is less than 2 m at both the outbound distances, with virtually identical slopes at both the distances.

Distribution of search lengths

The final analysis concerns the distribution of segment lengths. For this purpose, data from all ants at each outbound distance were combined. Data were placed in bins of approximately the same logarithmic size (0.05 log units) on

Table 1 Curves fitted to data shown in figures, their goodness of fit, and the Akaike information criterion (AIC) of the fits

Figure	Condition	y	x	$f(x)$	r^2	M error^2	AIC
4a	6 m, 31 turns	Midpoint	Segment number	$y = 5.37 \times x^{0.19}$	0.943	0.121	−20.9
4a	6 m, 31 turns	Midpoint	Segment number	$y = 0.008x^2 + 0.38x + 4.95$	0.984	0.028	−38.4
4a	12 m, 31 turns	Midpoint	Segment number	$y = 9.10 \times x^{0.22}$	0.975	0.140	−19.0
4a	12 m, 31 turns	Midpoint	Segment number	$y = 0.011x2 + 0.63x + 9.53$	0.994	0.044	−32.6
4b	6 m, 41 turns	Midpoint	Segment number	$y = 5.39 \times x^{0.21}$	0.936	0.193	−21.9
4b	6 m, 41 turns	Midpoint	Segment number	$y = -0.006x^2 + 0.37x + 5.49$	0.971	0.073	−37.3
6	6 m, power fit of all points	Log normalised freq	Log segment length	$y = -1.98x - 1.57$	0.836	0.168	−17.4
6	6 m, power fit of grey dots	Log normalised freq	Log segment length	$y = -0.80x - 1.47$	0.979	0.021	−40.9
6	6 m, power fit of black dots	Log normalised freq	Log segment length	$y = -4.12x - 0.05$			
6	6 m, exp fit of all points	Log normalised freq	Segment length	$y = -0.32x - 1.10$	0.978	0.023	−44.2
6	6 m, exp fit of grey dots	Log normalised freq	Segment length	$y = -0.33x - 1.08$	0.992	0.009	−52.3
6	6 m, exp fit of black dots	Log normalised freq	Segment length	$y = 0.07x - 5.15$			
6	12 m, power fit of all points	Log normalised freq	Log segment length	$y = -1.92x - 1.58$	0.891	0.111	−24.9
6	12 m, power fit of grey dots	Log normalised freq	Log segment length	$y = -0.95x - 1.51$	0.981	0.020	−44.9
6	12 m, power fit of black dots	Log normalised freq	Log segment length	$y = -3.34x - 0.48$			
6	12 m, exp fit of all points	Log normalised freq	Segment length	$y = -0.25x - 1.27$	0.944	0.057	−34.4
6	12 m, exp fit of grey dots	Log normalised freq	Segment length	$y = -0.31x - 1.13$	0.981	0.019	−45.7
6	12 m, exp fit of black dots	Log normalised freq	Segment length	$y = -0.10x - 2.91$			

The Akaike information criterion (AIC) is based on the residual error (M error^2; Burnham and Anderson 2002), and provides a ranking of models relative to one another (the lower the value the better). Model performance is based on the error relative to the number of parameters used in curve fitting. AIC = $n$log(error) + 2(r + 2), where n is the number of data points, and r is the number of free parameters used in curve fitting. Error = M error^2($n - r - 1$)/n. In Fig 6, when grey and black data points are separately fitted, the three columns on the right measure the two curve fits together

the x axis. On the y axis is the average relative frequency of the bin, averaged across all the linearly sized bins that make up each log-sized bin. The y axis is plotted on a log scale. The x axis is plotted on a log scale (top panels of Fig. 6) to examine the power law function, and on a linear scale to examine the exponential functions (bottom panels of Fig. 6). A linear function is fitted to the entire data set in each panel (in red). In addition, the data in each panel were also divided into a 'short' and a 'long' portion, and linear fits of each portion are shown in grey and black, respectively. The data were divided at the point (an additional free parameter) that provides the highest overall r^2 in each panel. Descriptive statistics of curve fitting are given in Table 1.

Examining the power function fits (top panels of Fig. 6), linear functions over the entire data sets provide poor fits, whereas two linear functions provide excellent fits at each outbound distance. The AIC was much better for the fits with double linear functions (Table 1). The two outbound distances had the break at the same point, the 2.6-m bin. At the right tails, the slopes are less than −3, falling outside the range between −1 and −3 said to characterize Lévy searches (Viswanathan et al. 1999). Thus, the search cannot be characterized as a Lévy process.

Examining the exponential functions (bottom panels of Fig. 6), single linear functions over the entire data sets

provide very good fits (Table 1). Dividing the data into short and long portions improves the fit as well as the AIC. This provides some evidence on grounds of model selection for Benhamou's (Benhamou 2007) theoretical optimal search consisting of two exponential distributions.

Yet we fear that in the case of the 6-m outbound distance, the double exponential distribution may be 'overfitting' the data (bottom left panel of Fig. 6). The long portion fits only three data points, and the slope is positive. A positive slope makes no theoretical sense, as longer search segments are supposed to be less likely. It looks like the black line is fitting the sampling error, and hence overfitting the data. This is made more likely by the fact that the slope for the short portion (in grey) is similar to the slope of the single linear fit (in red). One way to overcome the problem of overfitting data is to borrow the parameter for dividing the data into two portions from the data set on 12-m outbound distance. When the data set for 6-m outbound distance was divided at 6.5 m, the division point for the 12-m outbound distance (bottom right panel of Fig. 6), we obtain a mean squared error of 0.018, and an AIC of −44.6, similar to the AIC for the single exponential fit (−44.2, Table 1). Thus, on grounds of model selection, the double exponential function proposed by Benhamou (2007) characterizes the data well.
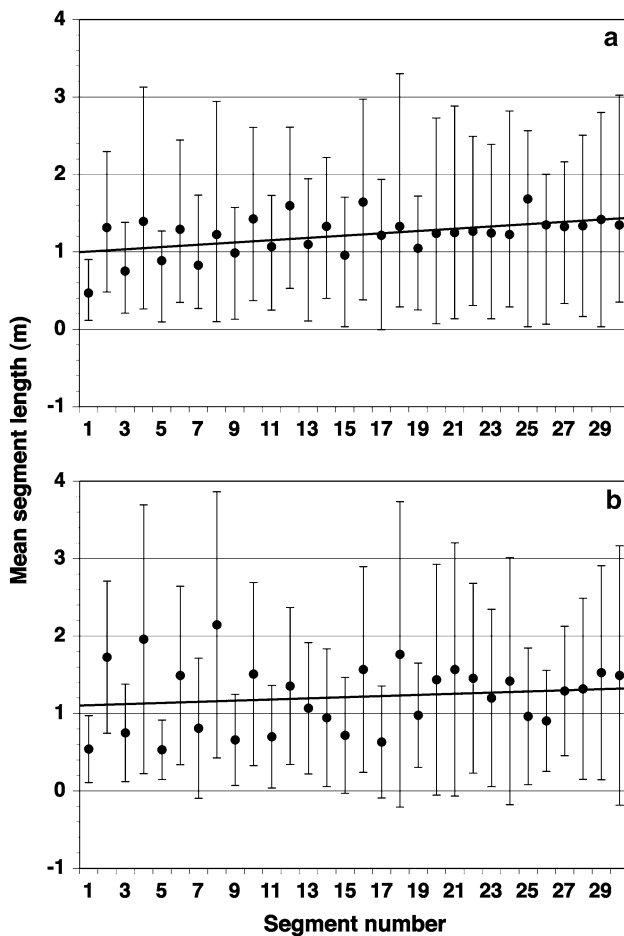
Fig. 5 Segment length along each of the first 31 turns for ants with **a** 6 m (*n* = 58) and **b** 12 m outbound distances (*n* = 22). Odd segments are directed towards the release point and even segments are directed away from the release point. Values shown are mean ± SD. Ants with fewer than 31 search segments were excluded from this analysis. A linear function fitted to the entire dataset is shown

average segment length increased slightly. The right tail decline of the distribution of segment lengths was well fitted by a power function, but the slopes less than -3 indicate that the process cannot be characterized as Lévy searches. A single exponential function over the entire data set (predicted for random Brownian movement) provided good fits to the data, but based on AIC, a double exponential function fits the distribution of segment lengths better, supporting an optimal pattern of search, the composite Brownian walk, proposed by Benhamou (2007).

The search strategy we found is novel. A comparable data set on the North African *Cataglyphis fortis* shows that after five training trials in a channel with both outbound and homebound distances of 6 m, no systematic forward drift was found (Cheng and Wehner 2002, Fig. 4). *C. fortis* shows a forward drift only when the homebound distance was manipulated to be longer than the outbound distance (Cheng and Wehner 2002). We discuss three possible hypotheses to explain the forward-drifting search in *M. bagoti*. (1) The ants might be using distant landmarks. (2) The asymmetry might arise from a learned route, in which the ants learn to go forward in the channel until they come to the nest enclosure at the end of the channel. (3) This search pattern might be a stereotypical feature of their search strategy and hence found in all the tested conditions.

Two previous studies have suggested that *M. bagoti* uses distant landmarks for navigation (Narendra 2007b; Wehner et al. 2006). Our study clearly shows that the forward search drift cannot be attributed to the use of distant landmarks, as ants released in the test channel adjacent to the feeder and those released in the test channel far away from the feeder exhibited similar asymmetric searches. Ants released adjacent to the feeder, after travelling the outbound distance estimated by their path integrator, would be immediately beside the nest. The landmarks visible from inside the channel at this point would look most similar to the landmarks surrounding the nest, visible from inside the nest enclosure and would become more dissimilar the further forward the ants drifted. Thus, any use of distant landmarks should have served to keep the ants searching in the region near the nest, which was clearly not the case.

Ants running in the channels might learn a sensorimotor instruction (Narendra et al. 2007a). Before arriving at the feeder, ants often ran back and forth numerous times in the outbound channel. Even the untrained ants, therefore, would have had some experience of running back home in a channel, providing them an opportunity to learn a sensorimotor rule such as 'run along the channel until it ends at the enclosure around the nest'. A tendency to run to the end of the channel might have produced overshooting, both in the distance that ants run before first turning back and also in the subsequent search (Cheng et al. 2006; Narendra et al. 2007a). Thus an instruction to keep moving forward could

Discussion

In this study, we analysed the search strategies of the desert ant *M. bagoti* by restricting their foraging in linear channels. The distance travelled by ants before beginning their search was similar to the distance they had travelled on their previous outbound journey. Ants exhibited a progressive search, moving gradually away from the first turn in the feeder-to-nest direction. Such an asymmetric search pattern was found in both naïve and experienced foragers, in ants from two different nests, and regardless of the starting point of the return journey, whether it was at the outbound distance from the nest or much farther away. The forward drift was modulated by the outbound distance: ants with 12 m outbound distance drifted farther than ants with 6 m outbound distance. Over the course of the search, the

Fig. 6 Distribution of segment lengths. In the *top row*, the *x*-axis is plotted on a log scale to examine the power law function. In the *bottom row*, the *x*-axis is plotted on a linear scale to examine the exponential function. The *y*-axis is plotted on a log scale in all *panels*. The linear function fitted to an entire data set is shown in *red*. Linear fits for data that were divided into short and long portions are shown in *grey* and *black*, respectively. This division was done at the point where r^2 was the maximum in each panel. Number of segments, 6-m: 3,935; 12-m: 1,797. Number of ants, 6-m: 141; 12-m: 70
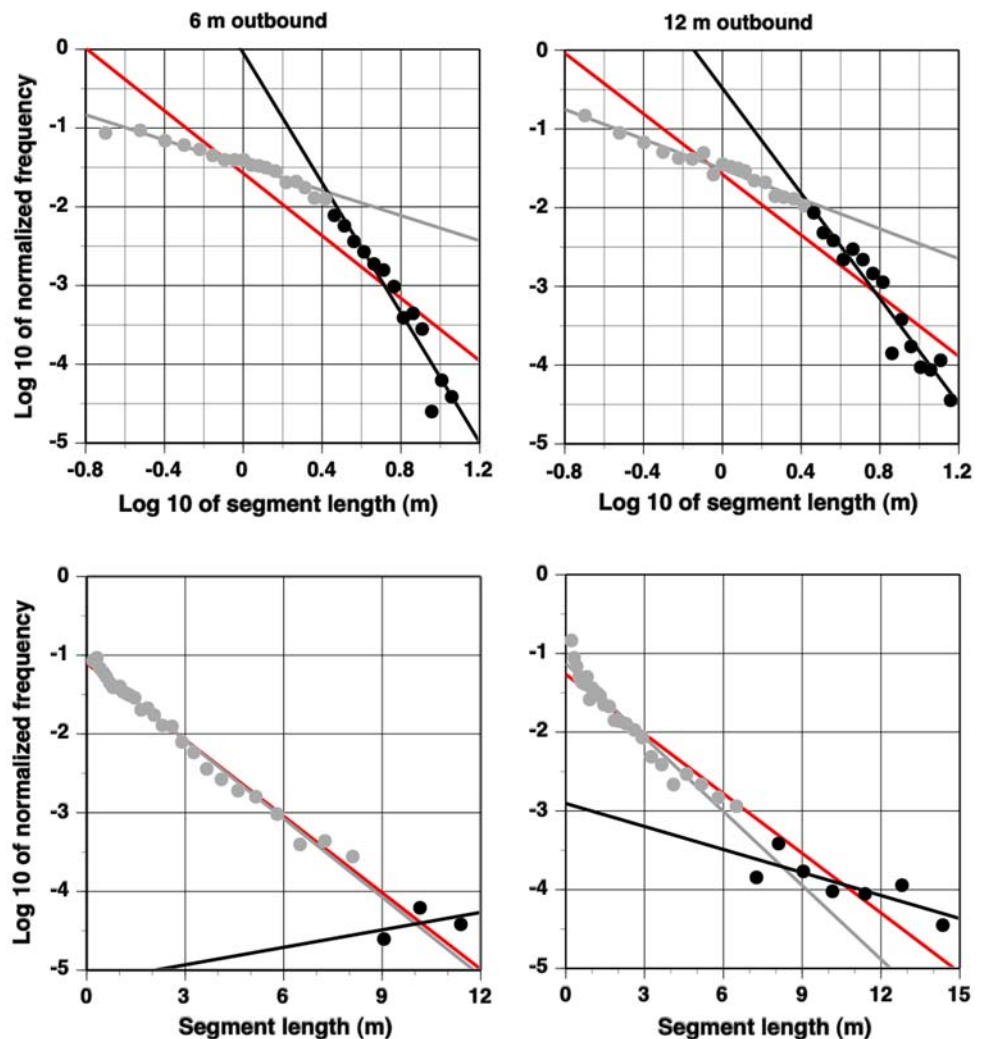
be superimposed on a symmetric search, resulting in a forward drifting search pattern. As ants with 12-m outbound distance may have given themselves more experience of turning back to the nest in the outbound channel before first arriving at the feeder than ants with 6-m outbound distance, they might have relied more on the forward-moving instruction, which is reflected by the larger drift in the search.

Travelling to and fro in the absence of familiar visual cues (as in channels) is an unlikely natural scenario for these ants. Hence, given that the asymmetric search pattern in this study is found under all the conditions, it might be a stereotypical behaviour. Drifting forward during search makes functional sense, since in an open unfamiliar field these ants travel only a part of the estimated homeward distance before starting to search (Narendra 2007a). If these ants typically search in an asymmetric pattern that includes a forward drift, this might apply even in the channel situation, where they travel the entire homeward distance before starting to search. Some evidence that the forward drift is stereotypical and also found in the open field comes from

the homeward trajectories of ants following nearby displacement (Narendra 2007b; Wehner et al. 2006). The amount of forward drift during the search may be a function of the travelled outbound distance. The ants' path integrator would continue to operate during search (Andel and Wehner 2004; Wehner and Srinivasan 1981), allowing the ant to monitor its forward drift. The path integrator might 'allow' a particular proportion of the initial outbound distance in forward drifting, to offset the errors that accumulate in the path integrator during the journey. So a longer outbound journey would accumulate more errors, and then lead to an increased forward drift during the search phase.

Further experiments are needed to distinguish between the learned-instruction and stereotypical hypotheses. Sensible manipulations include ensuring that the nest entrance is some distance away from the end of the training channel as in Knaden et al. (2006), or training the ants to a feeder over natural terrain, and then testing their return journey in a channel. In these paradigms, the stereotypical-behaviour hypothesis would still predict a forward drifting search pattern. The learned-instruction hypothesis would not. If the

nest is not at the end of the channel, the ants must learn the 'instruction' of travelling a particular distance to search for the nest. If the ants arrive at the feeder over natural terrain, they would have had no training in returning home in a channel, and no chance to learn any 'instructions'. Furthermore, search behaviour of these ants in a landmark-free habitat would be revealing (Wehner, Bühlmann, and Cheng, work in preparation).

So, why do *M. bagoti* ants have a progressively drifting search? Earlier work has demonstrated that these ants rely enormously on landmark information available in their habitat for navigation (Narendra 2007b; Narendra et al. 2007b). In the absence of familiar landmarks they resort to path integration but do not complete their entire home vector. The search of *M. bagoti* does not begin at the point where the nest is most likely to be located, but approximately half-way between the nest location and food source (Narendra 2007a). The progressive search exhibited by the ants is perhaps used to locate familiar visual cues along the route rather than the nest itself.

According to Viswanathan et al. (1999) and Bartumeus et al. (2002), Lévy walks may be expected only when the target density is low. The distributions of segment lengths in this study did not possess the characteristics of Lévy walks. The slopes of the power-law fits to the right tails were too steep. Similarly steep slopes have been reported for bumblebees searching in conditions of high-target density (Viswanathan et al. 1999), while bumblebees (Viswanathan et al. 1999) and honeybees (Reynolds et al. 2007) searching in conditions of low-target density have power-law tails with slopes nearer to the optimal -2. But in our case, the power law may not be the best characterization of the data at all. On grounds of model selection, the double exponential function performs somewhat better (Table 1). This pattern makes functional sense, as simulations have shown it to be highly efficient (Benhamou 2007; Plank and James 2008). In this regard, it would also be interesting to examine landmark-based searches, in which ants are trained with a constant array of landmarks around their nest. In *C. fortis*, for example, some landmark-based searches on a test field, far from the actual nest but having the landmark array, appear to be composed of concentrated searching at the location of the fictive nest according to the landmarks mixed with occasional wide loops of searching (Wehner 2003, Fig. 9; Wehner et al. 1996, Fig. 5). Such a pattern is qualitatively consistent with Brownian processes at two different scales, but a quantitative analysis would obviously be good to have.

Some caution should be taken in interpreting the data presented here. Our data set combined segments away from the start of the homeward journey and towards that point, and our other results have shown systematic differences between these segments. We think that this is unlikely to distort the pattern of search segment lengths. Variability in segment lengths is enormous in each direction of travel, each with many short segments interspersed with rarer longer segments. The test channel is a restrictive environment with a maximum length. On infrequent occasions, the ants would arrive at one of the ends of the channel: 4% of searches at the starting point, 10% at the far end, combining both the outbound distances. Although removing these searches would not affect the distributions much, these occasions might have artifactually limited especially the long segments, whose numbers are small to start with.

In summary, *M. bagoti*, an ant that inhabits landmark rich habitat, relies on a search that drifts progressively forward, irrespective of the degree of experience. They achieve this progressive search by alternating longer segments directed away from the release point with shorter segments aimed towards it. However, the average length of the search segments increased only a little as search progressed, suggesting a different strategy to the looping search of *C. fortis*. For the distribution of search segment lengths, a double exponential function fits best. This suggests a search consisting of two Brownian processes, one at a much smaller scale than the other. This is a pattern identified to be nearly optimal (Benhamou 2007; Plank and James 2008). The data do not support a Lévy search process. When fitted by a power function, the slopes at the right tail are less than -3, beyond the range of -1 to -3 stipulated for a Lévy search (Sims et al. 2008; Viswanathan et al. 1999).

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