Information content of visual scenes influences systematic search of desert ants

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Short title: Nest searching behaviour in desert ants
Summary

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.

Key words: 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 and 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 (Cheng et al., 2009; Collett et al., 2003; Wehner, 2003; Wehner and Räber, 1979; Wystrach et al., 2011a). Since the seminal works of Wehner and Räber (Wehner and Räber, 1979) and Cartwright and Collett (Cartwright and 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 and Cheng, 2009; Reid et al., 2011; Wehner and Müller, 2010; 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 (Philippides et al., 2011; Zeil et al., 2003). 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 and Collett, 2006; Müller and 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 (Durier et al., 2003; Narendra et al., 2007; Wehner and Räber, 1979). 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 (Müller and Wehner, 1994; Schultheiss and Cheng, 2011; Wehner and Srinivasan, 1981). 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 and Srinivasan, 1981). We also know that searching ants’ movements, i.e. the distribution of path segment lengths, follow a non-uniform pattern which is well described by a double exponential model (Narendra et al., 2008; Schultheiss and 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 setup

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 and 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, \textit{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 \textit{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).

\textit{IDF mapping}

We documented the visual surround of the nest using slightly modified methods of Zeil et al. (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 (Stürzl and Zeil, 2007; Zeil et al., 2003) for more detailed information]. Separate IDFs were created for the two experimental conditions.

**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 and 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. (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 and Rohlf, 1995)]. We fitted single function exponential and power law models to the complete data series. Distributions of exponential models follow
\[ f(x) = \lambda e^{-\lambda x} \] (1)
and those of power law models follow
\[ f(x) = x^{-\mu} \] (2).

Edwards (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 Eqn 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 and 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 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 ($M±SD$: 4.48±0.83%) than ants in the open condition ($M±SD$: 3.74±0.51%; $t$-test: $t_{124}=6.16, P<0.01$; 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. Fig. 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 Fig. 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 and 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 and 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).
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 (Durier et al., 2003; Narendra et al., 2007; Wehner and Räber, 1979). 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, 1998; Cheng et al., 1986), location of edges (Harris et al., 2007), spots of light or centre of gravity of objects (Ernst and 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 and 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 and 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 [Fig. 4 in (Schultheiss and Cheng, 2011)].

Although nothing is known about the underlying physiological mechanism, Wehner and Srinivasan (Wehner and 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 \textit{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 \textit{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.

\textit{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 and 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 \textit{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 \textit{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 and Srinivasan (Wehner and
Srinivasan, 1981), the ants’ search would be based on a single Gaussian \( a \text{ priori} \) probability distribution function. Similarly, \( M. \text{ bagoti} \) ants searching for a single food source at the end of their familiar outbound route also use a single exponential strategy (Schultheiss and 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 and 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 \( a \text{ priori} \) 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 and 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 \( M. \text{ bagoti} \) 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 \( \mu \) 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 and Cheng, 2011; Schultheiss and Cheng, 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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**List of abbreviations**

AIC  Akaike information criterion
IDF  Image difference function
MLE  Maximum likelihood estimate

**References**


Figure 1: Documenting the visual scenery around the nest entrance. (A) Overview of the experimental setup, viewed from approx. north-northeast. The setup 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. (D) Panoramic picture taken at the same location in the cluttered condition. Note that some of the added landmarks are hardly noticeable in front of the vegetation. (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.

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 or white 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 (open: N=70, cluttered: N=58).

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 SD, 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).
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).

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.
Table 1: Statistical parameters of function fits in Fig. 5. Calculation of maximum likelihood estimates (MLE) of model exponents follows (Edwards et al., 2007; Edwards, 2011). 95% confidence intervals (CI) were calculated with the profile likelihood-ratio test (Hilborn and Mangel, 1997), AIC with correction term (AICc), AIC weight, and evidence ratio were calculated following (Burnham and 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.

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<td>2.139-2.253</td>
<td>923.225</td>
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<td>4.390 $e^{-95}$</td>
<td>1.481 $e^{94}$</td>
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<th>Fit to tail end</th>
<th>exponent</th>
<th>95% CI</th>
<th>log-likelihood</th>
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<th>AIC weight</th>
<th>evidence ratio</th>
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<td>4.172</td>
<td>3.748-4.626</td>
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<td>3.721-4.611</td>
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<td>4.526-5.471</td>
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<td>0.020</td>
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