

The ontogeny of foraging behaviour in desert ants, *Cataglyphis bicolor*

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Abstract. 1. Individually foraging desert ants, *Cataglyphis bicolor*, exhibit short foraging lives (half lifetime, i.e. half-time of the exponential decay function: 4.5 days), in which they perform 3.7 ± 1.9 foraging runs per day.

2. During their short lifetime foraging period the ants increase the duration of their foraging round trips (up to 40.0 ± 24.6 min per run), the maximal distance of individual foraging runs (up to 28.2 ± 4.1 m), and their foraging success, i.e. the ratio of successful runs to the total number of runs (up to 0.70).

3. The parameter that increases most dramatically during a forager's lifetime is direction fidelity, i.e. the tendency to remain faithful to a particular foraging direction.

4. A model based on some simple behavioural rules is used to describe the experimental findings that within an isotropic food environment individual ants develop spatial foraging idiosyncrasies, and do so at a rate that increases with the food densities they encounter.

5. Finally, it is argued that in functional terms direction fidelity is related to the navigational benefits resulting from exploiting familiar (route-based) landmark information, and hence reduces round-trip time and by this physiological stress and predatory risk.

Key words. *Cataglyphis*, computer simulation, foraging ontogeny, sector fidelity.

Introduction

North African desert ants, *Cataglyphis bicolor*, exhibit short forager lifetimes and high colony turnover rates (Schmid-Hempel, 1983). Do foraging parameters such as round-trip time, foraging distance, success rate, or spatial aspects of the foraging runs vary during these short above-ground activities of the individually foraging ants? In particular, how does the direction fidelity that has been reported for *Cataglyphis* species (e.g. Wehner *et al.*, 1983), develop during a forager's lifetime?

Route and site fidelities have been described in many species of ants (Hölldobler & Wilson, 1990: 384–387;

Wehner, 1992). Individual ants may remain faithful to a particular trunk-trail route (e.g. *Pogonomyrmex* spp.: Hölldobler, 1976; Fewell, 1990; *Formica* spp.: Rosengren, 1971) and/or repeatedly visit a particular feeding site (e.g. *Camponotus noveboracensis*: Ebbers & Barrows, 1980; *Pachycondyla apicalis*: Fresneau, 1985). This kind of spatial specialisation occurs in individual foragers (e.g. *Cataglyphis bicolor*: Wehner *et al.*, 1983; *Pachycondyla apicalis*: Fresneau, 1985) as well as in mass-recruiters (e.g. *Pheidole militica*: Hölldobler & Möglich, 1980; *Messor aciculatus*: Onoyama, 1982), in the context of visually guided behaviour (e.g. *Pattothyreus tarsatus*: Hölldobler & Möglich, 1980; *Paraponera clavata*: Harrison *et al.*, 1989; *Cataglyphis bicolor*: Wehner *et al.*, 1996) as well as in olfactorily mediated orientation (see Harrison *et al.*, 1989 for the use of chemical vs. visual cues in *Paraponera clavata*), and it may persist for periods of weeks or even months (e.g. Rosengren & Pamilo, 1978). In nearly all studies performed

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so far, individual persistencies in spatial foraging behaviour have been ecologically correlated with spatial heterogeneities in the distribution of nutritional resources, especially with the occurrence of local patches such as aphid colonies (Ebbers & Barrows, 1980).

In the present account the ontogeny of direction fidelity and other foraging parameters in a species of ant that is characterised by *diffuse foraging* (Goss *et al.*, 1989; Traniello, 1989) is investigated. *Cataglyphis*, a strictly thermophilic scavenger (Wehner *et al.*, 1992) inhabits open and extremely food-impooverished desert terrains characterised by rather homogeneously distributed supplies of food (arthropod corpses; for the characterisation of the food environment at the study site see Schmid-Hempel, 1983; as well as the uniform distribution of nest sites within that area as documented by Dillier & Wehner, 2004). How and why is it, then, that these ants exhibit strong sector fidelities, even though they live within a non-patchy food environment? How is the spatial specialisation of foraging directions acquired during an individual's foraging life, and why has this behavioural trait evolved in the first place?

In trying to answer the first question, ants were labelled individually just when they commenced foraging behaviour, and the spatial layout of their successive foraging excursions and other foraging parameters throughout their entire foraging lives were recorded. Subsequently, the second question is tackled by referring to the constraints set by the ant's system of navigation.

Materials and methods

Study site and Cataglyphis species

All experiments were performed in the low-shrub semi-desert near Maharès, southern Tunisia (34.58°N, 10.50°E). Within this area about 30% of the sandy surfaces are covered with perennial chenopodiacean plants such as *Sueda mollis* and *Salsola tetrandra*. Receiving 100–200 mm annual rainfall, the study site is part of the presaharian North African Sahel zone (Floret *et al.*, 1982; Giessner, 1984). *Cataglyphis bicolor* (for species characterisation and biogeographical data see Wehner *et al.*, 1994) is a thermophilic scavenger collecting corpses of insects and other arthropods that have succumbed to the heat and desiccation stress of their desert environment.

Experimental establishment of cohorts of ants

In order to be able to precisely define the foraging age of an individual ant, two methods were used for establishing cohorts of ants.

(1) One nest of a polydomous colony of *C. bicolor* was excavated, and two samples of individuals were selected from the group of *inside workers* (Schmid-Hempel, 1983; Wehner *et al.*, 1983): *callows*, i.e. freshly hatched ants, which could be easily recognised by their pale yellowish cuticle,

and *repletes*, which serve as the colony's liquid stores and hence are characterised by their swollen gasters (Wehner *et al.*, 1972). After ants of either group had been labelled individually by using a three-colour code [Testor's PLA enamel colour dots applied to the head (occiput) and alitrunk (pronotum and propodeum)], the marked ants were re-introduced into the colony's main nest containing the queen (in the following referred to as the focus nest). This was done by releasing the marked individuals either directly into the opening of the nest or depositing them a few centimetres off the nest entrance. In the latter case the experimental animals were carried into the nest by their co-colonial nest mates. Subsequently the nest entrance was observed continuously by one person from the beginning to the end of the colony's daily activity periods, in order to enable the first above-ground appearances of the marked repletes and callows to be recorded. Two to three observers cooperated to acquire these data at the nest entrance. The first repletes and callows were observed to appear above ground and to start their exploration runs 5 and 11 days respectively after they had been introduced into the focus nest (Fig. 1a). In total ($n=46$), 68.2% and 25.0% of the individually marked repletes and callows respectively, could later be re-sighted as foragers.

(2) In *C. bicolor* the forager turnover rate is rather high, i.e. half of the forager force is replaced every 4.5 days (see below). As almost all active foragers appear above ground every day during their foraging lives (Schmid-Hempel & Schmid-Hempel, 1984), the following sampling method was applied during the course of this study. For two consecutive days all foragers of the focus nest were marked with a day-specific colour label. Consequently, on the third day all unmarked ants appearing at the nest entrance could be regarded as individuals starting their foraging lives. They were labelled individually by using the three-colour code mentioned above. Subsequently, all their foraging activities, e.g. the times when the labelled ants departed from and returned to the nest (departure times and arrival times), were recorded at the entrance of the focus nest over periods of up to 4 weeks. In addition, the trajectories of as many of their foraging runs as possible were traced out (recorded). At least two observers (one positioned at the nest entrance, the other(s) recording the spatial lay-out of the ants' foraging runs) were involved in these experiments.

The re-sighting frequencies of the marked foragers could be well fitted by an exponential decay function $N_t = N_0 e^{-\mu t}$ (Fig. 1b) with N_t and N_0 being the numbers of ants of a given cohort observed on day t and day 0 (the day at which any particular marked ant had started its foraging activity), and with μ being the mortality rate of the foragers. As a result, the half-lifetimes are 4.5 days, and the daily mortality rate is 15.4%.

Recording of sector fidelity

The directions of all outbound (foraging) and inbound (homing) runs of the individually marked ants were recorded

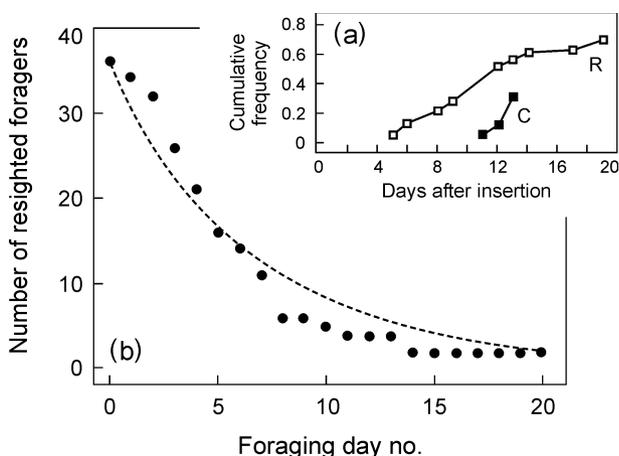


Fig. 1. (a) Cumulative resighting frequencies of individually marked ants belonging to two experimental cohorts (C, callows; R, repletes) that had been taken from a subsidiary nest of a *Cataglyphis bicolor* colony, inserted into the main nest of the same colony, and later checked for the beginning of their foraging activities (their first day of appearance above ground). (b) Survival curve of individually marked foragers. Two of the 36 marked foragers lived for more than 20 days.

by means of a reference circle (radius: 2 m) drawn around the entrance of the focus nest. The crossing points of the ants' foraging runs with the reference circle were determined (within 10° or 30° bins) and evaluated by Batschelet's (1981) statistics of circularly distributed data. The length r of the mean orientation vector is taken as a measure of sector fidelity: the larger r , the higher the sector fidelity. Values of $r = 1$ or $r = 0$ mean that a forager has occupied the same foraging sector over its entire lifetime, or that it has distributed its foraging activities randomly over all directions respectively.

In addition, complete foraging and homing trajectories were traced out on graph paper by using a 3-m square grid of white lines painted on the desert floor (polyvinyl-acetate dispersion paint, Flash) and an adequate grid printed on the recording paper. Time marks were set every 10 s. The observer following the ant at distances of 2–4 m did not influence the ant's foraging behaviour in any observable way. This conclusion is drawn from large sets of behavioural experiments, in which the ants' navigational abilities have been studied (e.g. Wehner, 1994). When while recording an ant's path the observer slowly changes his or her position relative to the ant, the ant's behaviour is not affected by this manoeuvre. In addition, the lines of the recording grid painted on to the soil had, if at all, only minor (and local) effects on the ants' paths and did not influence the geometry of their search pattern.

A 0.5-m square grid was established around the nest entrance (3 m × 3 m) in order to facilitate the recording of so-called *exploration runs*. Exploration runs are small-scale round trips about the nest entrance which precede the ants' foraging runs. During these runs the ants usually leave the nest entrance for less than 1–2 m and never collect food

items. In most cases, the exploration runs could be clearly distinguished from the subsequent foraging runs by their more convoluted spatial structure. In contrast, the foraging runs started with a rather straight, well-directed outbound trajectory. In operational terms, an individual ant's first run that crossed the reference circle ($r = 2$ m) was taken as foraging run no. 1 of that particular ant.

Upon return to the nest, the ant's foraging run was classified as *successful* or *unsuccessful*. In the former case the ants carried corpses of desert arthropods, or parts of such corpses, especially carcasses of desert isopods, bugs, and beetles; in the latter case no food item could be detected. An average of 40% of all recorded foraging runs ($n = 738$) were successful. In addition to gathering arthropod carcasses *C. bicolor* is known to lick plant surfaces and take in liquid food (Schmid-Hempel, 1983; Wehner *et al.*, 1983). In the present account, such *lickers sensu* Harkness and Wehner (1977) could not be distinguished from unsuccessful foragers; however, as at the Maharès study site licking occurs most frequently in the spring months (Schmid-Hempel, 1983), and as the experiments described in the present study were performed in the months of July and August (mainly in 1983, with additional observations during 1988–1994), the ratio of lickers to carcass collectors has certainly been close to zero. In fact, during the recording of individual search trajectories, no single case of licking was observed.

Computer simulations

Finally, computer models were used to test hypotheses about the experience-dependent changes in the ants' spatio-temporal foraging patterns. The foraging directions were simulated under various boundary conditions. The basic structure of the model, which is very similar to the one used by Deneubourg *et al.* (1987), has already been outlined in Wehner (1987).

The model incorporates the general observation that with increasing number of foraging runs, ants tend to restrict the spatial scope of their foraging activities to preferential directions. Foraging runs typically cover a fan-shaped area, a *foraging sector*, extending radially from the nest entrance: the ants leave the nest along a rather straight path, but as they venture out further, their paths get more and more convoluted and cover increasingly larger areas on either side of the main foraging direction (Wehner, 1987). Accordingly, the straightness of the foraging paths improves with experience. It appears that the tendency to stick to a given sector increases as a function of the number of previous successful runs, and that the tendency to switch to a random foraging direction decreases accordingly. These tendencies result in *sector fidelity*.

The model of sector fidelity uses three parameters to define boundary conditions:

D , the food density, given as the probability of finding a food item during a foraging run. An isotropic distribution of the food items around the nest is assumed.

T , the foraging lifetime of the ant given as the total number of foraging runs performed during an ant's lifetime.

τ , the half-time of the exponentially decreasing tendency to switch to a random sector after an unsuccessful run.

To simulate the spatiotemporal foraging pattern of an individual ant, the following variables are defined: t , time, measured as the number of foraging runs; $S(t)$, the number of successful foraging runs at time t ; $\phi(t)$, the foraging direction, measured in sectors of 30° , at time t ; and $p(t+1)$, the probability of switching to a random sector during the subsequent run $t+1$.

The model ant determines the foraging direction according to the following rules:

Rule 0: choose the first foraging direction $\phi(t=1)$ at random.

Rule 1: If the previous run was successful, stick to the previous foraging direction: $\phi(t+1) = \phi(t)$.

Rule 2: If the previous run was unsuccessful, select a new random foraging direction with probability

$$p(t+1) = e^{-\frac{\ln(2)}{\tau} S(t)}$$

Note that this *switching probability* decays exponentially as a function of the total number of previous successful runs, $S(t)$, while the total number of unsuccessful runs has no influence. In other words, the model ant does not increase its tendency to switch away from the preferred sector during unsuccessful runs.

As mentioned, the model system is characterised by the food density D , the ant's foraging lifetime T , and the strength of sector fidelity, as measured by τ . The resulting parameter space was explored for the following settings: *food density* (measured as the probability of finding a food item during a foraging run): $0.1 \leq D \leq 0.7$; *foraging lifetime* (measured as the total number of foraging runs): $3 \leq T \leq 30$; and *sector fidelity*: $0.25 \leq \tau \leq 16$.

For each parameter triplet, 3×10^5 foraging runs were simulated. These runs were performed by 10^5 ($T=3$) to 10^4 ($T=30$) individual ants, and the results were pooled over individuals.

To be compatible with the empirical results, the computer simulations were analysed with the same statistical methods as used in evaluating the ants' actual performances (computation of r -values, see next paragraph, below, and Fig. 7). In both cases, rather than focussing on the actual circular distribution of the foraging runs of individual ants, the first temporal derivative of that distribution is considered, i.e. the circular distribution of the term $\Delta r = r(t+1) - r(t)$.

Consequently, the interpretation of the circular statistics of Δr differs in some respects from that of r as defined by Batschelet (1981). In both cases random foraging yields a mean direction vector of length $r=0$, while complete sector fidelity yields $r=1$. However, since subsequent runs in the same direction all accumulate in sector $\Delta\phi=0$, independent of their absolute direction ϕ , ants exhibiting multimodal spatial distributions of their foraging runs would attain higher r -values than expected. However, the ants almost never selected more than one preferred foraging sector, so

that in practice the r -values computed in the present account have the same meaning as Batschelet's r -values.

In addition to the r -vector, the directionality of each individual's foraging behaviour was measured by the quantity R , the number of runs exhibiting sector fidelity $\Delta\phi=0$ relative to the previous run, expressed as a proportion of the total number of runs minus one ($T-1$).

Results

Exploration runs

An individual ant's outdoor activity starts with a number of one to three, rarely up to seven *exploration runs*. During these runs, which never last longer than 1–3 min, and often end after only a few seconds, the ants move at a rather slow pace, with their legs stretched and their antenna erected, in a number of loops around the nest entrance (Fig. 2). The most striking characteristics of these runs are the frequent turns, by which the ants repeatedly face the nest entrance. The turns are either full (360°) rotations about the ant's vertical body axis or partial ($<180^\circ$) rotations (followed by counterturns). While performing their exploration runs the ants are extremely sensitive to any kind of disturbance, e.g. to nearby movements of the observer, and immediately return to the nest whenever such disturbance events occur.

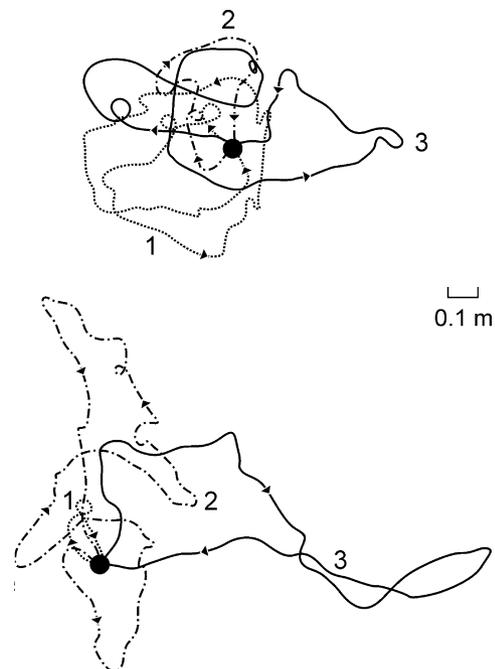


Fig. 2. Three successive orientation runs (runs nos 1–3) recorded in two ants immediately after the ants had first appeared outside the nest and started their foraging lives.

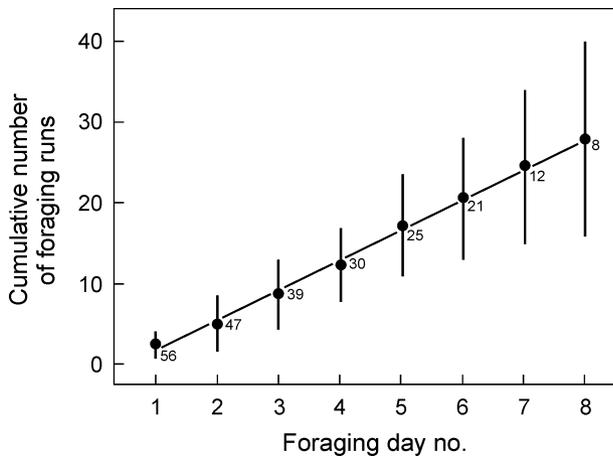


Fig. 3. Cumulative number of foraging runs performed by individual workers during their foraging life spans (number of foraging days). Means \pm SD are shown. The numbers next to the data points depict the numbers of individually marked ants recorded during the 8-day test period.

These runs have been termed *explorative* for two reasons. First they do not seem to serve any foraging function. Never did the ants grasp a food item placed in the vicinity of the nest entrance. Second, the rotatory movements, by which the ants turn back to the nest entrance, are a likely means of gaining some kind of spatial visual information (for *Formica rufa* see Nicholson *et al.*, 1999). Such turn-back rotations also occur, often quite frequently, at the beginning of a long-distance foraging run (for *Cataglyphis bombycinus* see Fig. 30 in Wehner, 1994). This is especially the case when the landmark scene around the nest entrance has been altered experimentally (R. Wehner, unpubl. data).

General characteristics of foraging ontogeny

On average, during 8 days of foraging life (the half-lifetime of the foragers is 4.5 days, Fig. 1b), the ants perform 3.7 runs per day. This is indicated by the slope of the regression line describing the cumulative number of foraging runs as a function of successive foraging days (Fig. 3; regression coefficient 0.83, $n = 238$). In total, during an 8-day period an individual ant would carry out about 30 forays (range 13–54) and provide the colony with 12 food items (see mean efficiency rate 0.40).

Spatial extent and duration of the foraging runs as well as foraging efficiency increase with the ant's foraging age (foraging lifetime). Averaged over its entire foraging life, an individual ant's foraging round trip would last, on average, for 40.4 ± 30.6 min (mean \pm SD). The duration of the foraging runs increases from runs 1–3 (23.8 ± 20.5 min per run, $n = 110$) to runs 4–6 (40.0 ± 24.6 min per run, $n = 107$) ($P < 0.01$, two-sided t -test, $t_{215} = 2.60$), but then remains

constant for all further (up to 33) foraging runs. Along with the duration of a foraging run (Fig. 4a) it is also the ant's maximal distance from the nest that increases with foraging lifetime (Fig. 4b). Whereas the ants leave the nest for a maximal distance of only 8.4 ± 5.9 m ($n = 26$) during their first foraging runs (runs 1–3), they do so for 28.2 ± 4.1 m ($n = 5$) during their last ones (runs 28–30) ($P < 0.001$, $t_{29} = 3.66$). If a circle with a radius of 20 m is drawn around the nest entrance, all runs 1–5 remain within that circle ($n = 41$), while in runs 25–30 two-thirds of the ants (67%) venture beyond that circle ($n = 10$). In successive foraging runs the ants adopt what appears to be two distinct strategies: either to concentrate their search at the previous finding site, or to pass this site and venture out further (see also Schmid-Hempel, 1983).

The parameter that increases most dramatically with forager lifetime is foraging efficiency, i.e. the ratio of the number of successful runs to the total number of (successful and

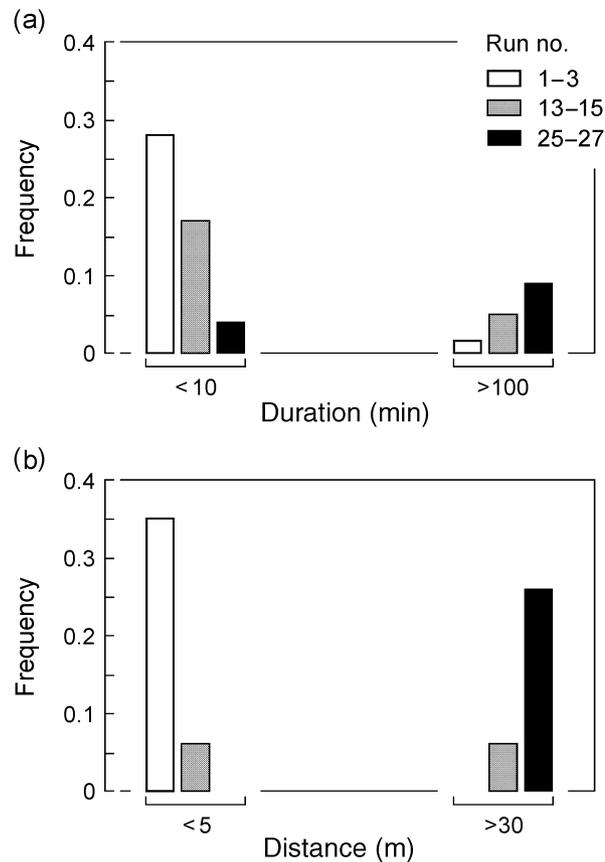


Fig. 4. Frequency distributions of (a) the durations of the foraging runs, and (b) the maximal distances covered during these runs for different age groups of foragers. Runs nos 1–3 and nos 25–27 signify the beginning and the end of a forager's lifetime respectively. The frequency distributions are presented only for the shortest runs (duration < 10 min, distance < 5 m) and the longest runs (duration > 100 min, distance > 30 m). $n = 150$ (runs nos 1–3), 75 (runs nos 13–15), and 27 (runs nos 25–27).

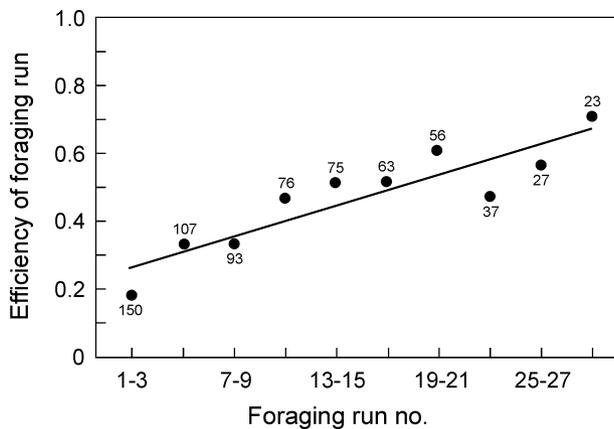


Fig. 5. Foraging efficiency as a function of foraging age (number of foraging runs per individual ant). Efficiency is defined as the ratio of successful runs, i.e. of runs in which a food item has been found, to the total number of runs. The small numbers next to the data points represent the numbers of foraging runs recorded in ants of any particular age class. The correlation coefficient of the linear regression is 0.89.

unsuccessful) runs. As shown in Fig. 5, foraging efficiency increases from 0.19 for runs 1–3 ($n = 150$) to 0.70 for runs 28–30 ($n = 23$) ($P < 0.001$, $t_{171} = 3.35$). One could argue that the 12 ants (23 runs) scoring highest in foraging efficiency during the end of their foraging lives have been the most successful ones already from the very beginning of their outdoor activities. Such is not the case. If only the longer-lived ants are considered, e.g. if all ants performing less than 12 runs are excluded, the efficiency rates do not differ from the ones shown in Fig. 5 ($P \gg 0.1$ for all three-run cohorts, $n = 104 \pm 24.0$ runs per cohort, χ^2 test). Hence, the long-lived ants, which later in life reach the highest efficiency rates, score as lowly at the beginning of their foraging lives as the short-lived ants do. The mean foraging efficiency for all recorded runs 1–30 ($n = 738$) is 0.40, but if the first three runs are excluded, i.e. if only runs 4–30 ($n = 557$) are considered, efficiency reaches 0.45 and hence comes close to the values of 0.50 and 0.52 reported by Wehner *et al.* (1983) and Schmid-Hempel (1983) respectively. As will be shown in the next section, foraging efficiency is strongly correlated with sector fidelity.

Sector fidelity

The most remarkable feature of the spatial layout of the foraging activity of *C. bicolor* is that in successive foraging runs each individual ant tends to leave the nest in one particular direction, but that different individuals select different directions. Hence, the individual ants partition the foraging ground of their colony. How is this partitioning achieved, i.e. how does an individual ant select its foraging sector?

A first hint towards answering this question comes from a comparison of Fig. 6a and b (see also Fig. 7). Ant no. 233 (Fig. 6a) was successful only once (during run no. 9) during its first 18 foraging runs, while ant no. 214 (Fig. 6b) scored at least 10 (perhaps 13) times during its first 34 runs (during runs 5, 6, 9 [?], 14, 18 [?], 19, 22, 23 [?], 25, 27, 29, 30, and 33; the convention [?] behind the run number means that the observer was not able to record beyond any doubt that the returning ant carried a – sometimes very small – food item; most likely, however, the ant did). What strikes the eye immediately is that the former, extremely unsuccessful ant (efficiency rate 0.06) did not develop any sector fidelity, whereas the latter, more successful ant (efficiency rate 0.29–0.38, see above) clearly did. However, it seems to be this below-average efficiency rate that causes the overall spatial foraging pattern even of the latter ant to be less focussed on a particular foraging direction than is usually the case (see, for instance, figs 12–15 in Wehner *et al.*, 1983).

Obviously, as can be deduced from the foraging histories of the two ants mentioned above, sector fidelity is correlated with foraging efficiency, and as the latter is a function of forager lifetime (Fig. 5), sector fidelity can be expected to increase with lifetime as well. This is indeed the case and nicely borne out in Fig. 7, in which sector fidelity is depicted in two ways: (1) as the length r of the mean vector of the ants' outbound courses measured at the reference circle, and (2) as the percentage of runs, in which individual ants have remained faithful to the same 30° sector they had selected in their previous run, or in which they had chosen one of the two adjacent 30° sectors. As the spatial distributions of an ant's foraging directions are almost always unimodal, i.e. as an ant channels in on one mean foraging direction, repeatedly selecting the previously visited foraging sector means sticking time and again to the very same foraging sector. Measures (1) and (2) correspondingly show that sector fidelity strongly and rapidly increases with foraging lifetime.

What rules do the ants apply in choosing their finally permanent foraging sector? From inspecting quite a number of foraging histories of individual ants the following hypothesis can be derived: The ant chooses a random foraging direction for its first run. If this run has been successful, the ant sticks to this (30°) sector during its subsequent foraging run. On the other hand, if this run (and the subsequent runs) has (have) been unsuccessful, the ant randomly selects a new sector, but the tendency to switch to a random direction decreases exponentially with the number of preceding successful runs.

Take, for example, the foraging life history of ant no. 233 portrayed in Fig. 6a. This ant, which had been successful only once during its first 18 foraging runs, did not develop any sector fidelity, but its run no. 10 following the only successful run no. 9 led directly to the former feeding site. In contrast, run no. 9 itself deviated by more than 90° from its unsuccessful predecessor. However, if the ant had already been successful a few times during its foraging life, the probability of an unsuccessful run leading to the random selection of a new sector is reduced considerably. For example, ant no. 513 (Fig. 8a) exhibited sector fidelity

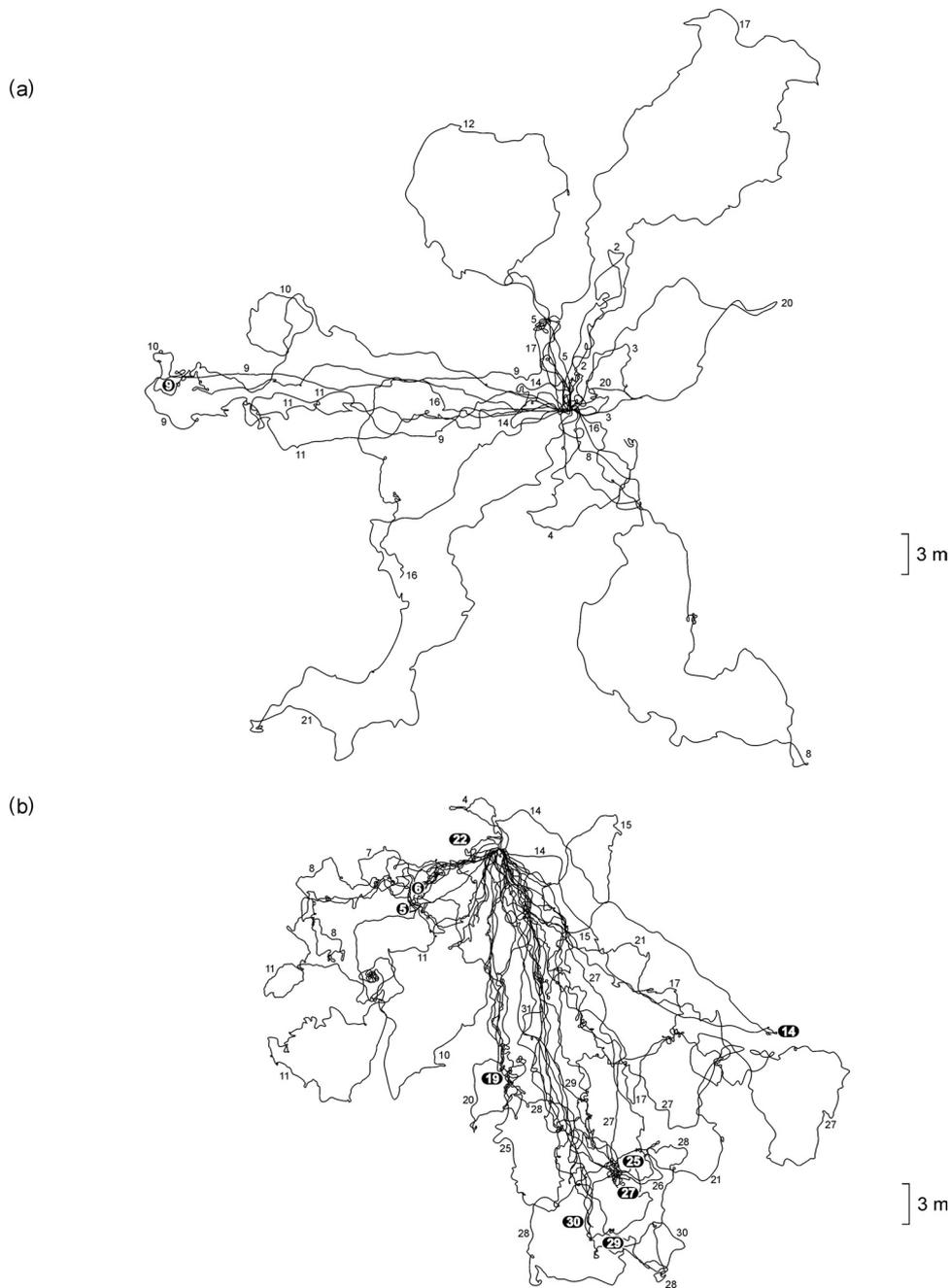


Fig. 6. Spatial distribution of successive foraging paths in two individual ants. In the one ant [(a), ant no. 233] the trajectories of 18 of the first 22 foraging runs have been recorded. In the other ant [(b), ant no. 214] the trajectories of 24 of the first 34 foraging runs were recorded. Ant no. 233 (a) had been especially unsuccessful in scoring only twice during its first 22 foraging runs (runs nos 9 and 19; the trajectory of the latter could not be recorded). Even after 22 runs, this ant did not exhibit any sector fidelity. Ant no. 214 (b), which had been more successful than ant no. 233 (at least five, perhaps seven times during its first 22 foraging runs; see text), developed a higher sector fidelity. The numbers of successive foraging runs are printed next to the ants' trajectories (small black numbers). The large numbers shown in white on a black background depict the locations where the ants have been successful, i.e. where a food item has been found.

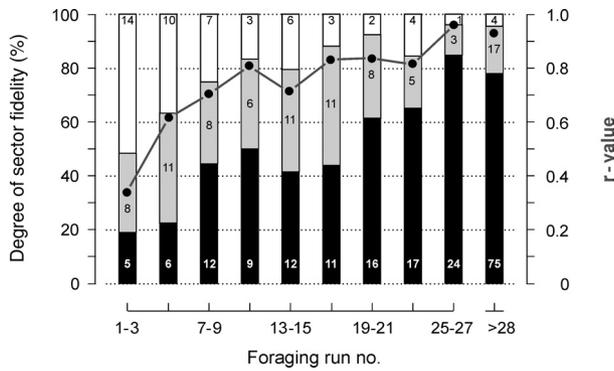


Fig. 7. The acquisition of sector fidelity during foraging lifetime (abscissa: number of foraging runs per individual ant). The data are presented in two ways. First (left ordinate, histograms), the percentage of ants selecting the same 30° sector (black bars) or an adjacent 30° sector (grey bars) as in their preceding foraging run is shown. White bars indicate that the ants selected other foraging sectors than the ones mentioned above. Absolute numbers are given inside the bars. Second (right ordinate), the filled black circles connected by bold line segments denote the r -values as computed from the ants' circular distributed foraging directions (according to Batschelet, 1981). A value of $r = 1.0$ means that all ants selected the same foraging sector during their foraging runs (in three-run bins). The other extreme, the case of $r = 0$, means that the ants did not acquire any sector preferences at all.

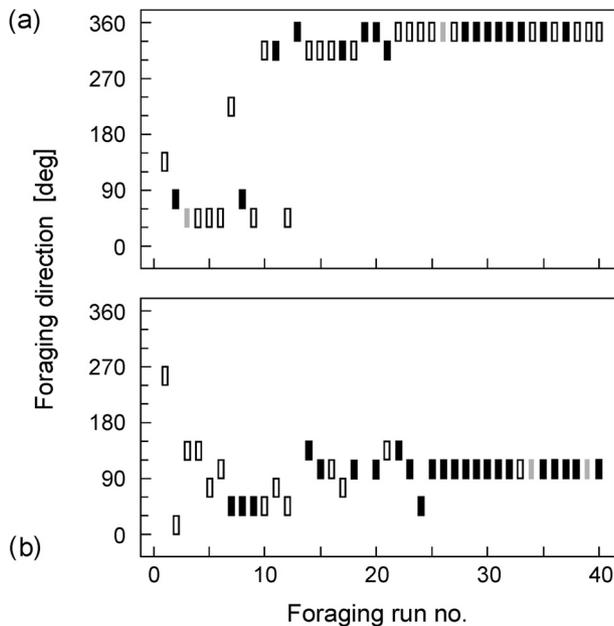


Fig. 8. Foraging directions chosen by ant no. 513 (a) and ant no. 512 (b) in successive foraging runs. Foraging directions are given in 30° bins. The black and white vertical bars denote successful and unsuccessful runs respectively. When no clear-cut decision could be made by the observer, a grey bar is presented instead.

even during three to four unsuccessful runs in a row (runs 14–16, 22–25), after it had previously been successful four to five times (runs 2, 3 [?], 7, 11, and 13).

Modelling sector fidelity

A computer model has been designed to test how a number of parameters such as the density of food D (an external parameter) or the half-time τ of the exponential decay function describing the ant's switching probability (an internal parameter) might affect a forager's development of sector fidelity. The model assumes that the acquisition of these directional specialisations is mediated by a number of rather simple behavioural rules (see also Deneubourg *et al.*, 1987) such as stick to a foraging sector if you have been successful within this sector during the immediately preceding foraging run, and switch to a randomly selected new sector if at the beginning of your foraging life you have returned from an unsuccessful journey, but do so with exponentially decreasing probability the more often you have been successful during preceding foraging runs. These rules predict that two parameters should speed up the acquisition of sector fidelity: (i) high food densities, i.e. high encounter rates of food items, and (ii) the rapid exponential decay of the tendency to switch to a random direction after an unsuccessful run. Figure 9 depicts the results of computer simulations based on the behavioural model rules mentioned above. In particular, it shows how directionality develops during an ant's foraging lifetime T as food density D and switch rate τ are varied systematically (for details see Material and methods; let it be mentioned in passing that the curves displayed in these graphs do not represent individual acquisition curves, but data from individuals with different life-spans, corresponding to the structure of the empirical data set).

Rather than seeking a perfect correspondence with the empirical data, the principal aim of the model calculations is to obtain an estimate of the parameters D and τ characterising the behaviour of real foragers. The food density D can be estimated from the empirically determined proportion of successful runs relative to the total number of observed runs. In the case of *C. bicolor* at the Tunisian study site, this estimate results in a mean value of $D = 0.4$. The simulations for $D = 0.4$ (Fig. 9b) show a time course similar to the empirical data for values of $\tau < 1$, indicating that the ants acquire sector fidelity rather rapidly, i.e. during the first few successful runs.

While the acquisition of sector fidelity is modelled here as a function of previous successful runs, it might be argued that – in the sense of a leaky memory – sector fidelity decays over time. Assuming a temporally limited memory, sector fidelity may be modelled as a function of the number of successful runs S' during the previous runs h ($h = t$) rather than during all previous runs t . Model simulations show that the empirical curve of Fig. 9 can be approximated with

$h=8$. This suggests that the time horizon during which individual foragers integrate successful runs is relatively large, extending back to about a third of an average forager's lifetime.

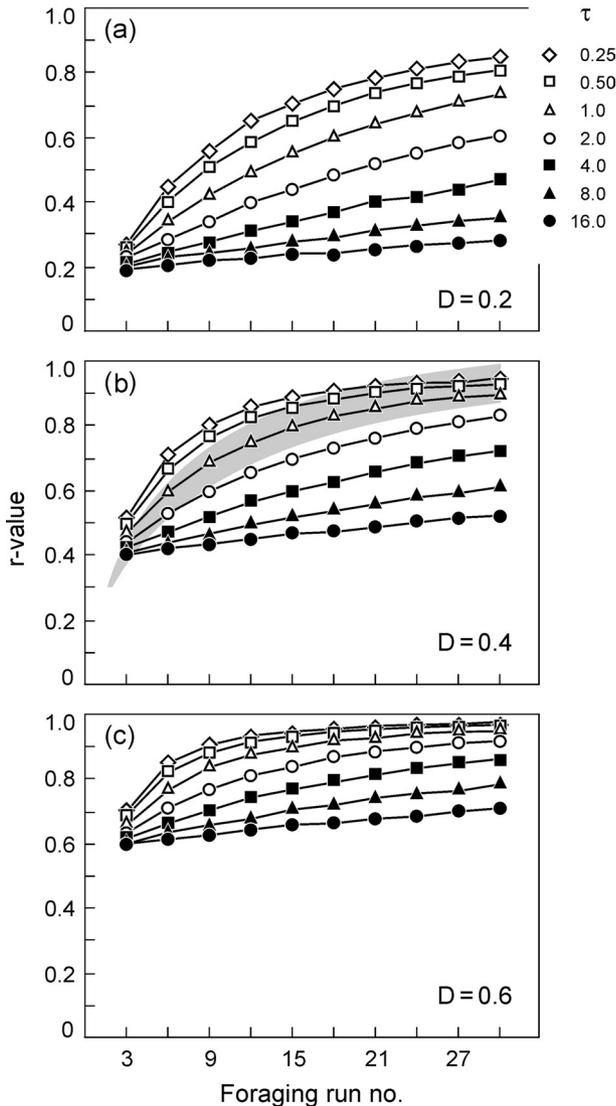


Fig. 9. The acquisition of sector fidelity as derived from computer simulations (for model, see text). Sector fidelity is measured by the length, r , of the mean vector of the circular distribution of foraging runs (Batschelet, 1981). The families of curves presented in (a), (b), and (c) apply to different food densities, D , as reflected by the ants' foraging efficiencies. Each graph displays the directionality r for values of τ ranging from 0.25 to 16 (τ is defined as the half-time of the exponential decay function describing how the ant's probability to switch to a random sector after an unsuccessful run decreases with foraging lifetime). The grey area in (b) (for $D=0.4$ as pertaining to the Tunisian study site) represents the r -values for the empirical data (see Fig. 7). Its course suggests natural values of $\tau < 1.0$.

Discussion

The development of sector fidelity during a forager's lifetime

Sector fidelity, i.e. the tendency to stick to a previously selected foraging direction (or sector), is rather rapidly acquired during the lifetimes of individually searching desert ants, *C. bicolor* (see, for example, Figures 7 and 8). This empirical finding is also borne out by the model presented in the last section of the Results part. Furthermore, the model is in accord with the naturally varying food densities as they occur in different desert habitats. In a preliminary study of the foraging behaviour of *Ocymyrmex velox*, which inhabits the gravel plains of the central Namib desert, a food encounter rate of $D=0.18$ yields much weaker foraging directionalities, i.e. much smaller values of r , than described in the present account for *C. bicolor* in North Africa (Wehner, 1987). On the other hand, a Greek population of *Cataglyphis nodus* (species status still to be established) exhibits encounter rates of $D=0.9$ and, accordingly, extremely high sector fidelities (Wehner *et al.*, 1983).

In conclusion, individual foragers of *C. bicolor* acquire pronounced spatial specialisations in their foraging directions by applying a set of simple rules rather than by spatially examining the entire foraging range of their colony. These rules guarantee that as foraging lifetime proceeds an individual ant will stick to an idiosyncratic foraging sector even if previous foraging runs have been unsuccessful in retrieving food items from this sector. Very few successful runs suffice for strong direction persistence to develop.

Rather than relying on (in fact inaccessible) global knowledge about the profitabilities of particular parts of a colony's entire foraging space, the ants succeed in partitioning this foraging space by applying local rules. These local rules also explain that a colony's forager force can quickly adapt to inhomogeneities in spatial food supplies (see, for example, Fig. 18 in Wehner *et al.*, 1983). Ants that by chance have commenced their foraging activities in a rich sector rapidly develop persistency to this sector, while ants having started out in poor sectors continue switching directions until at least a fraction of them does also end up in the rich sector. If recruitment occurred as, for example, in trail laying *Lasius* ants (Beckers *et al.*, 1990) or in foraging honey bees (Seeley, 1995), this sector concentration effect would be largely amplified. Nevertheless it is surprising to see how effectively even the diffuse (non-interactive) foraging mode is able to exploit heterogeneously distributed food supplies.

The functional significance of sector fidelity within an isotropic food environment

Why do ants living under – at least statistically – isotropic food distribution conditions exhibit spatially anisotropic foraging activities? Ecologically speaking, it would not matter whether in an isotropic food environment any particular ant kept randomly switching its foraging direction after any

particular foraging run or whether – as is actually the case – particular ants remained faithful to particular directions, with all ants of the colony covering all directions.

To answer the question posed above, a number of additional factors influencing an individual ant's overall foraging efficiency, such as the amount of energy invested to retrieve a unit amount of food per unit time, must be considered. From this perspective, in addition to the actual foraging success (E in the model) various environmental factors bear on the overall performance of the forager itself, such as the time spent outside the nest or the total distance travelled.

As a general strategy it is sensible to reduce these *travel risks* by shortening round-trip time, i.e. to forage in an already known sector rather than search in random directions. Observations and experiments on the ants' navigational strategies clearly show that within a cluttered environment *Cataglyphis* can develop landmark-guided idiosyncratic foraging routes based on visual signposts and local vectors attached to them (Wehner *et al.*, 1983, 1996; Collett *et al.*, 1992, 1998; Bisch & Wehner, 1998). When displaced sideways, the ants first adopt a search course, but once they hit their familiar route, they quickly follow it back to the nest (Wehner, 1990; M. Kohler and R. Wehner, unpubl. data). Such landmark-based homing strategies considerably decrease round-trip time and thus reduce physiological (heat and desiccation) stress as well as predatory risk. The latter are the factors responsible for the foragers' short (4.5-day half-) lifetimes. In contrast, in the laboratory colonies *C. bicolor* workers may stay alive for periods of several months or even years. In short, sector fidelity is certainly related to the navigational benefits resulting from sector familiarity. It should be added, however, that *C. fortis*, which is an endemic species of the North African salt-pan flats, develops the same type of sector fidelity even in landmark-free environments (R. Wehner, unpubl. data). Hence, sector fidelity improves navigational performances depending on route-based memories, but its ontogenetic development is not necessarily linked to the presence of landmarks.

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