

1. Perspective

The neurobiology of insect navigation has focused either on neurophysiological analyses of the sensory capacities involved or on model descriptions of how the whole system could work theoretically. What has not kept pace with the progress made in both the neurophysiological and cybernetic approach, is a proper understanding and appreciation of the ecological conditions which any navigational system must meet. In general, the physiologist is abysmally ignorant of such needs. It even reflects the tone of physiology in relegating observations made in the field of behavioural ecology to the level of interesting curiosity. This deliberate oversight is aided and abetted by the very nature of physiological and cybernetic research – to inquire about the general rather than the particular case.

In following this line one might well miss a crucial point. Trying to understand the *neurophysiology* of navigation and orientation, indeed of any kind of behaviour, is the obvious, if distant goal of many research programmes. However, what recent physiological analyses can provide at best is how certain kinds of sensory information are preprocessed by peripheral neural subsystems. Work on identified interneurons is proceeding apace, and patterns for fitting such interneurons together will begin to emerge (e.g. Hoyle, 1977; Hausen, 1981; Pearson, 1980, 1982); but by proceeding step by step from peripheral to more central neuropiles one will soon encounter considerable difficulties in interpreting the wealth of neurophysiological data in functional terms.

In this state of affairs, many have started at the other end by analysing the stimulus/response characteristics of a particular kind of *behaviour*, and defining the stimulus conditions which the brain needs in mediating the response. In recent years, promising and fascinating results have been obtained by following this approach, especially in the field of visually guided behaviour (e.g. Reichardt, 1970; Goetz, 1975; Collett and Land, 1975; Reichardt and Poggio, 1976; Cartwright and Collett, 1982; Wehner, 1982a,b; Rossel and Wehner, 1982). Nevertheless, we must admit that our current knowledge might just barely be adequate to explain how the animal behaves in the sterile visual world of the laboratory rather than how it copes with the richness of information available in its real world.

In providing model descriptions of neural networks, the *cybernetic approach* sets out to bridge the gaps left by neurophysiologists and behavioural scientists. In particular, it tries to design networks that mediate a given behavioural response as parsimoniously as possible (e.g. Mittelstaedt, 1978). However, bound to the irrelevant standards of our own conceptions, we have no a priori way to decide what standards a given insect species must meet.

only way to come to grips with such questions is to inquire about the *behavioural* ecology of the species. It is that need which this account endeavours to fulfil. At this point, however, we have neither a party-line nor a totally encompassing theoretical position to offer. What we present instead is a case study focusing on the foraging ecology of one of the most remarkable desert insects, the ant *Cataglyphis bicolor*. What is known about how these ants navigate by visual means, and how their visual systems are designed (for summaries see Wehner, 1981a, 1982a). But when we started our investigation, we knew nearly nothing about the ecological requirements which have shaped the ant's system of navigation. Hence, we decided that it would be well worth somebody's while to go out to the desert to have a look.

Species

Cataglyphis bicolor is well suited for such an enterprise. It is a large, speedy ant found in arid regions of the Old World, including North Africa, the Mediterranean area and the Near East. Several behavioural traits make this ant an ideal object for combined studies in the fields of neurobiology and behavioural ecology.

Like all members of the genus, the ants are scavengers searching for widely scattered food items. They are solitary foragers never engaging in mass foraging along scent trails. While foraging, each ant works completely on its own. There appears to be no social commitment, and inter-individual encounters, either cooperative or aggressive, rarely occur.

Because of their large size and conspicuousness, the ants are easy to follow when they walk, though rapidly in full sunlight, over the bare ground of their arid habitat. They are also easy to label individually by coloured tags.

Successive foraging trips of individual ants can be recorded over periods of days and weeks, in fact over the entire lifetime of a forager. Each ant performs only a few foraging trips per day, which may last for up to two hours and may lead the ant for up to several hundred meters away from the nest. Thus, the foraging activities of individual ants can be studied in spatial and temporal details.

At any one time, in a colony there are not more than a few hundred foragers, so that the foraging activity of a substantial fraction of the whole forager force can be recorded. This, in turn, allows us to assess the spatio-temporal organization of the foraging activity not only of an individual ant, but of the entire colony as well.

Most decisively, *Cataglyphis* ants are diurnal foragers hunting over the desert landscape and at the hottest times of the day. In navigation, they rely nearly exclusively on visual cues including skylight patterns and landmark panoramas. As the navigational abilities of these ants have been amply studied for many years, experimental procedures are at hand allowing us to record the foraging and homing paths of these ants under natural or experimentally modified conditions.

3. Objectives

Most of the studies concerning foraging in ants focused on remarkable phenomena such as group hunting in army ants (Rettenmeyer, 1963) or trunk trail formation and mass foraging in seed-harvester ants (Hoellndobler, 1976). In addition, economically more important species have received vivid interest, such as wood ants (Rosengren, 1977) or leaf-cutting attini (Weber, 1972; Wilson, 1980). Much less is known from ants employing a «diffuse foraging» technique (Oster and Wilson, 1978). This strategy is normally considered to be restricted to the more primitive subfamilies, e. g. ponerinae and myrmecinae ants, but it is just this kind of individual foraging that the highly advanced formicine ants of the genus *Cataglyphis* employ.

The fact that *Cataglyphis* ants are individual foragers has been the starting point of the present investigation. Two main topics are considered:

(1) *Foraging strategies: Spatio-temporal organization of individual foraging runs.* The spatial and temporal aspects of the foraging activities of individually marked ants are studied in detail. It has been a central aim of our field investigations to record successive foraging paths of individual ants over extended periods of time. Data about the extension, duration, geometry, and site-fidelity of the foraging trips are derived from these records and discussed in terms of the distribution of the widely scattered food items exploited by the ants. The question we will raise is how foraging patterns relate to the distribution of food that is in general highly unpredictable in both space and time (see also Schmid-Hempel, in prep.).

To underpin any conclusions drawn from the foraging data two populations of *Cataglyphis bicolor* occurring in quite different habitats (Tunisia and Greece) are compared. This comparison will provide information on how the species can mould its foraging system in response to different environmental requirements. What will emerge is that certain key parameters of the foraging system are maintained at both sites, but that this is accomplished by very different means.

(2) *Navigational strategies: What kind of map is used?* Foragers leaving the nest and searching individually stimulate the question of how these ants find their way to a particular food source, and back to the nest. Given the often extreme inconspicuousness of the nest entrance – a small hole barely visible on the desert ground – the question of homing is especially intriguing in these ants. The navigational strategies employed by *Cataglyphis* are dead reckoning (vector navigation by means of a celestial compass; Wehner, 1982 a) and piloting by landmarks (Wehner, 1981a; in press). A more detailed analysis of the foraging runs will reveal that individual ants repeatedly return to one, two, or more locations where they have been successful before. Here the question arises as to what kind of map is used by the ants. Do they pilot on landmark maps in the same way as human navigators? How is such a map established?

and read? Or, alternatively, do they use a vector map where foraging sites are defined by polar coordinates with the nest as the origin? Some of these problems have already been tackled by training ants to artificial landmark configurations (Wehner, in press). However, what is needed first and foremost is more detailed information about how *Cataglyphis* performs in its natural environment. Only then will we be able to judge of the full navigational abilities of these ants, and propose hypotheses about the nature of the ant's map.

II. Material and Methods

1. Study Sites

The ants were studied at two sites about 1250 km apart from each other, and separated by the Mediterranean Sea: in the Presaharan arid zone of North Africa, near the village of Maharès in southern Tunisia (34.58°N, 10.50°E)¹, and within the historic scenery of northern Thessalia, Greece, near the town of Platamon (40.00°N, 22.37°E). The location of both sites with respect to the distributional range of *Cataglyphis bicolor* is depicted in Map 1.

In their general appearance, both study sites can be described most readily as shrub deserts covering the alluvial plains near the seashore. Some 10–20 per cent of the surface are sparsely covered with small bushes. In Tunisia, shrubs consist mainly of *Sueda mollis*, *Salsola tetrandia* (Chenopodiaceae), and *Nitraria retusa* (Zygophyllaceae), whereas in Greece *Quercus fruticosa* (Fagaceae) is the dominating perennial plant. The residual ground is almost void of any vegetation (Tunisia) or partly covered with annual grass plants and patches of *Artemisia scoparia* (Compositae) (Greece) (Fig. 1).

Even though both sites selected for comparison look rather similar in terms of coverage by vegetation, there are marked differences concerning other geographic variables. At Maharès, the area under investigation is part of the desert shrub zone characterizing the whole Tunisian Sahel for hundreds of square kilometres. All river beds (oueds) are free of water during the summer months. At Platamon, however, the study site is surrounded by the slopes of Mt. Olympos (2917 m) and Mt. Ossa (1978 m), which are densely covered with bushes (the so-called Greek phrygana) and deciduous forests. Reed and willows grow on the pediment plains of these mountains, some hundred metres off the experimental area. Many rivers (e.g. Peneios) contain water all the year round, though most of the smaller rivers and water courses do dry up in summer. Obviously, there are distinct climatic differences between the Tunisian and Greek study sites. At Maharès, summer temperatures are considerably higher and annual precipitation values much lower than at Platamon. At noon, in August, air temperatures range from about 35° to 45° at Maharès and from 25° to 35° at Platamon. Annual rainfall is between 100 and 200 mm at Maharès, but between 800 and 1000 mm at Platamon. According to Creutzburg's classification of climatic zones (Bluethgen, 1980), 3 and 1 humid months are assigned to the Tunisian and Greek study site, respectively. Due to these climatic differences, the area in Greece is much more productive. This can be deduced directly from the average annual rainfall which is known to be a sufficiently precise indicator of net primary production in arid regions (Rosenzweig, 1968). As is

¹ For geomorphological and hydrographic classification of this area see Despois (1940), Mensching (1968) and Floret et al. (1982).

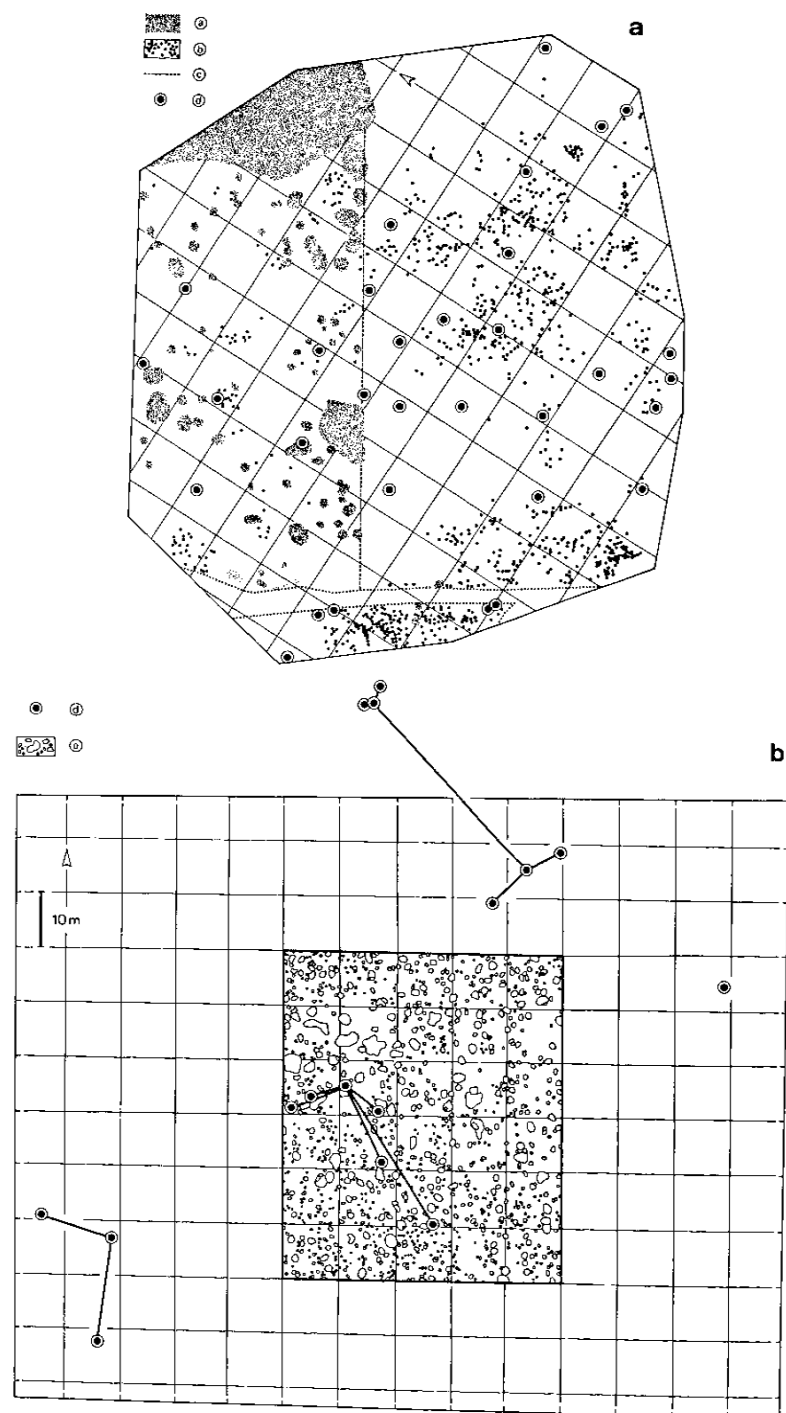


Fig. 1

will be shown later in detail, the density of potential food items available to *Cataglyphis* foragers is indeed much higher in Greece than in Tunisia.

A further difference between the two study sites which will turn out to be of utmost importance with respect to foraging patterns and foraging capacity, relates to the presence or absence of congeneric competitors. In Tunisia, another *Cataglyphis* species, the smaller *Cataglyphis albicans*, is present within the same habitat. As this sympatric species subsists on the same kind of food and applies the same foraging strategy, it acts as a potential competitor to *Cataglyphis bicolor* (Schmid-Hempel, in prep.). On the other hand, *Cataglyphis cursor*, the ecological substitute for *Cataglyphis albicans* in southern Europe, is not present at Platamon.

2. Taxonomy

Comparing two populations of conspecific ants occurring at different geographical locations requires some consideration of what taxonomic status must be assigned to each population (see Plates 1 and 2 following p.10). This is all the more important as the taxonomy of the genus *Cataglyphis* has suffered regrettable neglect since the turn of the century. Forel (1902), Emery (1906), and especially Santschi (1929) have described and named an uncanny abundance of species, subspecies, and variations of forms belonging to the *Cataglyphis bicolor* complex. For example, at the same site amidst the Tunisian steppes between Kairouan and Le Kef, *Cataglyphis bicolor* ssp. *bicolor* var. *basalis* and *Cataglyphis bicolor* ssp. *nodus* var. *desertorum* are described as occurring side by side.

All this profligate naming was due to an extreme overemphasis on what taxonomists call splitting. What resulted were almost unworkable keys relying on a number of rather variable characteristics such as worker size and coloration. The variation of these characteristics was never checked, and most descriptions were based on single «type» specimens. Even though this unwieldy taxonomy, lacking any touch of population and evolutionary biology, has been harshly criticized by Brown (1955), the genus *Cataglyphis* has later attracted the attention of taxonomists only once (Arnoldi, 1964). Unfortunately, this latter attempt was restricted to material from Asia, and was nearly exclusively based on the morphology of the male genitalia. On the other hand, Forel and Santschi (lit. cit.) collected *Cataglyphis* ants in North Africa and the Near East, and relied on morphological characteristics of worker ants only. Thus, the taxonomic studies at hand hardly help in answering the question posed above.

Fig. 1: Maps of the study sites at Platamon GR (a) and Maharès TN (b). The arrow points towards north. The mesh width of the grid is 10 m. (a) Ground covered mostly by shrubs of *Quercus fruticosa*; (b) Individual plants of *Artemisia scoparia*; (c) borderline between grassy area (northwest) and bare sandy ground (southeast); (d) nest sites of *Cataglyphis bicolor*; solid lines connect nests belonging to the same colony; (e) bushes, consisting mainly of *Sueda mollis*, *Salsola tetrandia*, and *Nitraria retusa*. In b coverage by vegetation is depicted only for the central part of the area under investigation.

vertheless, what are we left with when exclusively referring to those studies? According to Santschi's (1929) system the Maharès and Platamon populations must be regarded as different subspecies of *Cataglyphis bicolor*: *Cataglyphis bicolor bicolor* and *Cataglyphis bicolor nodus*, respectively². The evidence for this distinction, even when restricted to the subspecies level, is very slim and mainly based on worker coloration. The dark Tunisian forms are referred to as *Cataglyphis bicolor bicolor*. The term *Cataglyphis bicolor nodus* is assigned to the lighter Greek forms all characterized by a conspicuously orange-red colour of the heads, the alitrunk, and the legs, contrasting sharply with the black gaster. In fact, however, such «bicolor» forms also occur in North Africa where they are typical of the Atlas Mountains and the Mediterranean north of these mountain chains³. Based on specimens from our own collection (R. W.), the geographical distribution of these colour varieties has been mapped for Tunisia (Map 2). A similar map can be provided for Algeria. The most striking feature of such distributional maps is the rather sharp boundary between the light forms in the north and the dark ones farther south. But this is not a point to be considered here. The emphasis is only placed on the fact that the coloration of the ants occurring in northern Tunisia and Algeria is indistinguishable from that of the Greek specimens. Against this background it might appear surprising that Arnoldi (1964) described the Greek (and Turkish) forms as a separate species (*Cataglyphis nodus*). However, as in this paper no reference is made to the classic *Cataglyphis bicolor*, there is no way of knowing in what respect the male genitalia, Arnoldi's sole criteria, differ between both species. In fact, comparisons of the Tunisian forms (own collection, Zurich [R. W.]) and the Greek and Asian forms (Arnoldi's [1964] drawings; Forel's collection, Genève; collection of the British Museum of Natural History, London) do not reveal consistent differences.

There is one further morphological parameter which has turned out to be of great taxonomic importance in the rapidly running ants of the genus *Cataglyphis*: the relative length of femur and tibia (see Wehner, 1981b). On the basis of this parameter, it is possible to discriminate clearly between all *Cataglyphis* species known so far (Wehner, 1981b, unpublished). However, data taken from Tunisian and Greek specimens follow the same regression line when plotted against head width. The ratios $F = \text{femur length}/\text{head width}$ and $T = \text{tibia length}/\text{head width}$ do not differ significantly between the Tunisian and Greek specimens. For the hind legs these ratios are $F_m = 1.84 \pm 0.10$ S.D. (n = 84) [Maharès] and $F_p = 1.82 \pm 0.10$ S.D. (n = 37) [Platamon] ($p > 0.32$). The

² A similar classification has been used by Forel (see Forel's *Cataglyphis* collection at the Musée d'Histoire naturelle in Genève). Santschi was even less consistent in discriminating between both subspecies in geographical terms, in that some varieties of *Cataglyphis bicolor nodus* were considered to occur in North Africa.

³ Originally, these light forms have been described as *Cataglyphis [Formica] megalocola* by Foerster (1850). Santschi (1894) referred to them as *Cataglyphis [Myrmecocystus] bicolor [viaticus] ssp. megalocola*. This classification was later adopted by Emery (1906) and Stitz (1917), but was abandoned by Santschi (1929).

corresponding numbers for the tibia are $T_m = 1.80 \pm 0.09$ S.D. (n = 84) and $T_p = 1.77 \pm 0.09$ S.D. (n = 57); $p > 0.57$. These numbers refer to medium-sized specimens (head widths 1.8–2.0 mm). No statistically significant differences can be found in the middle legs and forelegs either.

In conclusion, according to direct comparisons of ants from both study sites, and an evaluation of all characteristics used by former taxonomists, we are convinced that the North African and Greek populations belong in fact to the same species, *Cataglyphis bicolor*⁴. The question whether subspecies names should be assigned to either population is one of alpha-taxonomic taste. As geographical separation isolates both populations, it is somewhat sophisticated anyway. Furthermore, with respect to foraging strategies as compared and discussed in this paper, there is no need for further taxonomic differentiation between the Greek and Tunisian forms.

3. Experimental Procedures

The data were collected over several years at both study sites. To ease comparisons, all data presented in this paper refer to the same time of the year – the month of August. In Tunisia *Cataglyphis bicolor* foraging activity reaches its maximum during the summer months (June–August). During that time all foraging parameters considered in this investigation, especially the spatial and temporal organization of the foraging activities of individual workers, do not vary consistently.

In this Section, only some general experimental procedures are mentioned. The gadgets and strategies used in particular tests are described in detail at the appropriate places in Chapter III.

Due to the large size of *Cataglyphis bicolor*, the workers can be labelled individually. The colour code used is easily read in freely walking ants. Labelling was accomplished by providing the alitrunk or gaster with coloured dots using shellac, aluminium paint or Testor's PLA enamel. As in any particular colony there is only a limited number of workers searching for food (see Section III. 3.b), a substantial fraction of this total forager force of a colony can be labelled. A 3-dot code including five different colours was employed, which allowed for 125 ants to be discriminated individually. In each colony studied, a random sample of workers active at the nest was marked.

In the Tunisian area, a 3 m-square grid was painted directly on the ground. This grid proved useful in many ways. It facilitated the recordings of individual foraging paths as well as the survey of the nest sites. In Greece, individual ants were followed and their positions marked on the ground, at constant intervals of time, with numbered aluminium or plastic labels. The positions of the marks were determined later by measurement from a set of fixed reference points.

⁴ In this context it should be mentioned that Schneider (1971) as well as Chhotani and Ray (1976), though not dealing specifically with taxonomic questions, use the notation *Cataglyphis bicolor* for populations occurring even farther east than Arnoldi's (1964) form *Cataglyphis nodus*.

Following, foragers searching for solid food items (mainly dead arthropods) will be called *searchers*. Their foraging paths were recorded by taking fixes (records of position) every 10, 30, or 60 sec. For a survey of the temporal activities, the departure and arrival times were taken at a reference circle drawn around the nest entrance (radius 2 m).

As to the searchers some of the foragers are neither searching for nor taking solid food items. Instead, they are licking secretions from plant surfaces. These foragers will be called *lickers* whenever it is necessary to distinguish them from searchers. They return repeatedly (often over their entire lifetimes) to the same plant, and thus they do not search».

During navigational strategies, whole nests were displaced to areas where the ants were not yet familiar with the landmark surroundings. This was done by moving the nest at the end of the day when all the foragers had returned and any foraging activity had stopped. By means of a modified vacuum cleaner, the ants were collected individually. Immediately, the whole population was transported to a new site where it was released within a completely shielded cage provided with a substrate in its bottom. The population was then given the opportunity to dig a new nest by starting from the tube. Usually, the ants completed the construction of the new nest the same night. Next morning, the shielded cage was removed and a training set of artificial landmarks was installed around the entrance of the new nest. In most cases, the landmarks consisted of two black cylinders, 38 cm high and 22 cm wide, placed at a distance of 2 m apart from the nest entrance. The ants were allowed to become familiar with the training situation for one day. Then, workers were tested during another 3–6 days in experimental areas at different distances from the training area.

Statistics are described in the appropriate sections. Unless mentioned otherwise, means and standard errors are given.

Plate 1 and 2: Cataglyphis

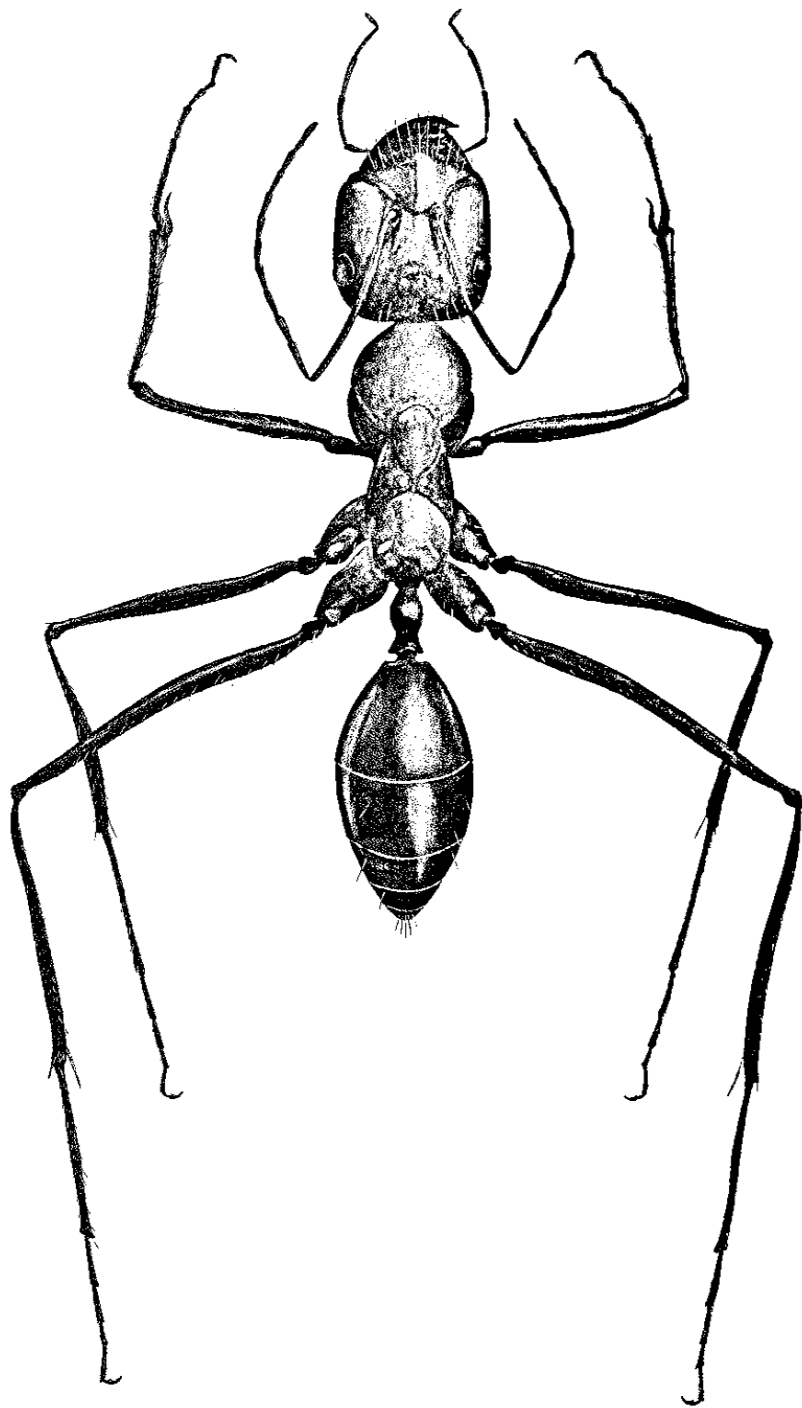


Plate 1: *Cataglyphis bicolor*, ♀, Maharès, Tunisia.
See Map 2b for geographical distribution of this type of coloration within Tunisia.

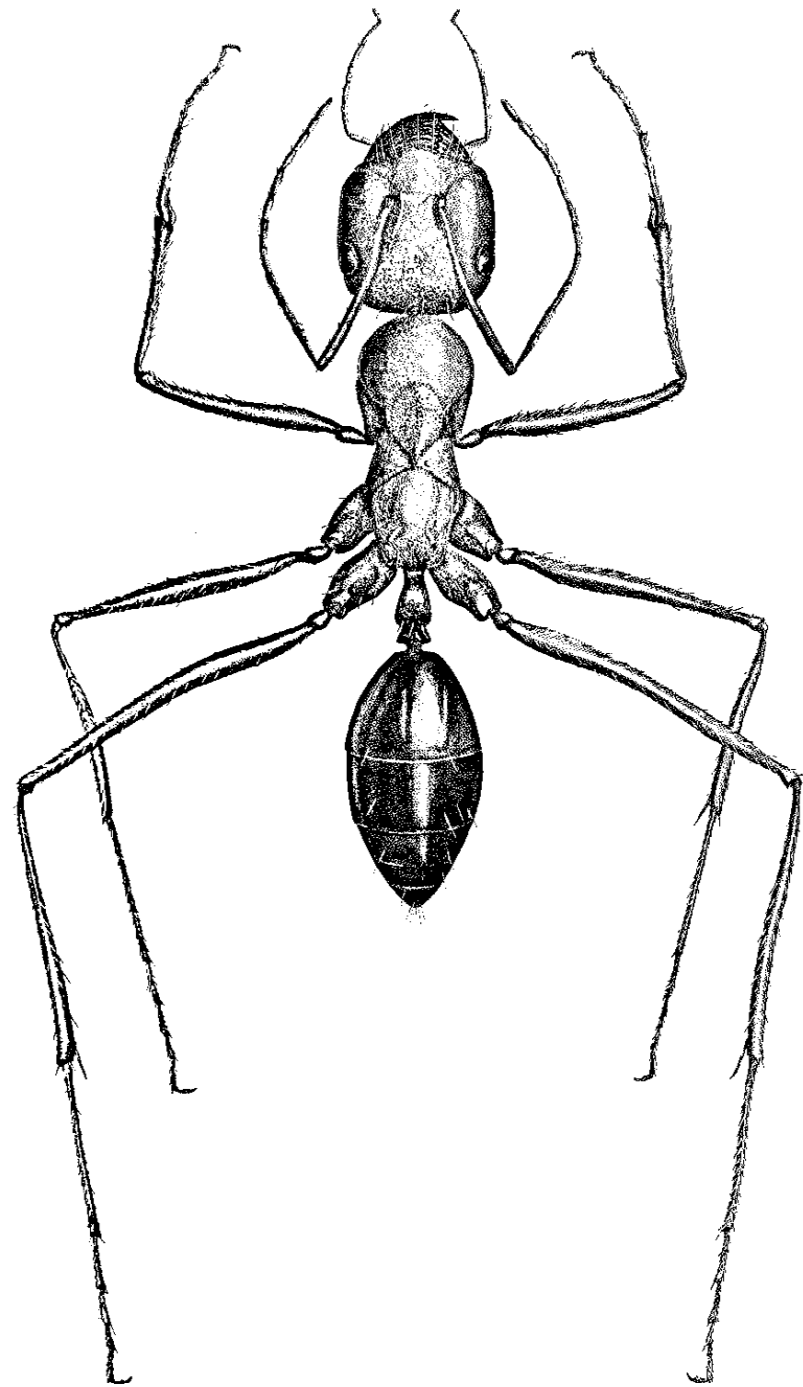


Plate 2: *Cataglyphis bicolor*, ♀, Platamon, Greece.
See Map 2a for geographical distribution of this type of coloration within Tunisia.

III. Results

The main topic of this investigation relates to the spatial and temporal organization of the foraging activities of individual ants (Chapters III.4 and III.5) and to how the individual foraging strategies employed by the ants mesh with the navigational strategies by which each ant finds its way (Chapter III.6). To provide the proper ecological background for tackling such questions, the interdependence of the mode of foraging and the distribution of food will be discussed first (Chapter III.1), followed by a consideration of how the abundance and distribution of food items within the ants' environment is reflected in the size and the spacing of the colonies (Chapter III.2). Observations and experiments on the life history dynamics of *Cataglyphis bicolor* are important for interrelating foraging behaviour and navigational strategies employed. These aspects are discussed in Chapter III.3.

1. Mode of Foraging and Type of Food

Without any doubt, foraging is among the most important activities an animal must perform. This holds particularly for the exterior workers of social insects, since these individuals are not engaged in other activities such as searching for mates. Therefore, it is to be expected that the behaviour of workers outside the nest will be dominated by the need to search for food.

a) *Methods.* Usually foraging ants do not consume a food item at the finding site but instead carry it back to the nest where it is delivered to the colony. Hence, a dietary analysis is relatively simple: Returning foragers are captured and the food item carried with their mandibles removed. Any forager returning within a given period is sampled in this way. The fresh weight of each food item is measured using a precision balance (Mettler PC 180 or Oerting 48), and assigned to one of the following groups which can easily be distinguished: (1) Isopods, (2) ants, (3) bugs and beetles, (4) caterpillars, (5) flying insects, (6) plant material, and (7) miscellaneous.

The workers do not find a suitable food item on every foraging run. Foraging efficiency is defined as the ratio of the number of successful runs to the total number of runs occurring within a certain period of time. Runs are considered to be successful if the ants are returning with a food item held in their mandibles. Obviously, this ratio applies only to the intake of solid food. To estimate to what extent materials are carried in the crop (as opposed to carried in the mandibles), foragers must be observed during their entire foraging trips. Only then are we truly able to decide whether the foragers are searching for dead arthropods or licking plant material. In Greece, where lickers accounted for a much larger percentage of foragers than in Tunisia, lickers and searchers could be distinguished readily by their behaviour on leaving the nest. Characteristically, the lickers walked at a steady continuous pace in nearly a straight line to a

bush into which they climbed (and were lost to view). Individual ants constantly worked either as searchers or lickers.

b) *Mode of Foraging.* Foragers of *Cataglyphis* leave the nest independently of each other and search for food individually. This mode of foraging holds for both study sites. In addition, there is no evidence for any efficient recruitment mechanism. The foragers carry back just one food item at a time, and the size of the item is generally limited by what a single forager can carry or drag by itself⁵. As far as their foraging is concerned, individuals are confined to the same nest even if the colony comprises more than one nest.

c) *Type of Food.* *Cataglyphis bicolor* is a scavenger. Its food consists of a wide range of dead arthropods. The ants were rarely observed to subdue living organisms, which moved around actively. Occasionally, living larvae, *Messor* reproductives, or bugs remaining motionless when threatened were taken. In Tunisia and Greece, some 60 to 80 % of the items consisted of dead isopods or ants, respectively (Tab. 1). In Tunisia, the isopods occurred frequently within the experimental area, whereas in Greece dead ants (mainly *Messor* spp.) were the most abundant prey available. At the latter site, for every one *Cataglyphis* nest in the area there were about two *Messor* spp. nests. Thus, the regional differences in food can readily be accounted for by the different types of

Table 1: Relative frequencies (per cent) of various taxonomic groups in the diets of *Cataglyphis bicolor* at both study sites. The composition of the diets varies significantly between Greece and Tunisia (Chi-square test, $p < 0.001$).

Group	Greece N = 51	Tunisia N = 89
Isopoda	2.0	52.8
Formicidae	68.6	10.1
Hemiptera, Coleoptera	19.6	7.9
Lepidoptera (Larvae)	2.0	7.9
Lepidoptera, Diptera (Imagoes)	2.0	4.5
Plant Material	0	14.6
Miscellaneous	5.9	2.2

⁵ In theories of «central-place» foraging, in which animals repeatedly return to a central place, e. g. the nest, this mode of foraging is known as «single-prey loading» (Orians and Pearson, 1979).

food available at the study sites. *Cataglyphis bicolor* does not seem to exhibit preferences for any particular kind of prey. The ants appear to retrieve rather indiscriminately what is available to them at any one time.

When in Greece, on occasion, large numbers of reproductives leave the nests of harvesting ants (*Messor* spp.) over a short period of time, these reproductives are collected in great numbers (up to two per minute over a period of one to two hours) by large *Cataglyphis* workers. Usually, the live males and females are taken whole but gaster or head may be removed.

In Tunisia, the ants collect berries of *Nitraria retusa* in addition to animal matter. Licking of plant exudates and of crystallized excretions of aphids is frequently observed in June. It occurs almost exclusively on bushes of *Nitraria retusa*. In Greece, however, licking seems to be much more important. There, licking is observed frequently throughout most of the study period (end of July to beginning of September). It occurs on small *Crataegus* shrubs, *Quercus* spp., *Tribulus terrestris*, *Euphorbia chamaesyce*, *Heliotropium europaeum*, *Xanthium spinosum*, and *Artemisia scoparia*.

d) *Food Consumption and Foraging Efficiency.* Since the desert isopods (*Hemilepistus reaumuri*) collected in Tunisia are on the average much larger than the dead animals that ants collect in Greece, the different types of prey lead to quite different quantities of food intake at the two study sites. The fresh weight of an average food item retrieved in a successful run is 5.8 ± 1.0 mg ($n=56$) in Greece, but 39.6 ± 4.3 mg ($n=89$) in Tunisia. Considering the number of foragers per colony (Section III.3.b), a colony of *Cataglyphis bicolor* collects roughly 5 g of solid matter per day in Greece, but 30 g per day in Tunisia.

Yet only about half the foraging ants return to the nest carrying solid food items. This figure is roughly the same at both study sites. Among workers returning without solid food items, some have licked dry plant surfaces and would be transporting liquid food in their crops. In Tunisia, however, the body weights of foragers which had returned without solid food items in their mandibles did not differ significantly from the body weights of foragers returning with loads. In Greece, a small difference could be detected. Thus, we conclude that in Tunisia licking does not contribute much to the intake of food. This conclusion is confirmed by following individual foragers within their foraging areas. None of the 35 workers of which full path records were taken in August were observed to lick plant surfaces. In Greece, however, a presumably great share of the «unsuccessfully» returning workers have taken liquid food while foraging. As berries are not collected at the Greek study site, there the supply with equivalent (carbohydrate) food seems to be secured by licking alone.

e) *Occurrence of Food.* Food distribution is determined by a number of independent factors. This is especially true for the food items collected by a scavenger. Carcasses should occur rather unpredictably. As far as our data indicate this is indeed the case. In Tunisia, food occurs mainly within or at the boundaries of shrubs which are dispersed

over the foraging range of the ants. In Greece, the places where ants find food items are generally scattered in the area in a way which appears to be random: Dead *Messor* ants are found close to as well as far away from the nests (Fig. 2). Thus, at either study site *Cataglyphis* ants do not encounter a clumped or any other predictable pattern of food distribution.

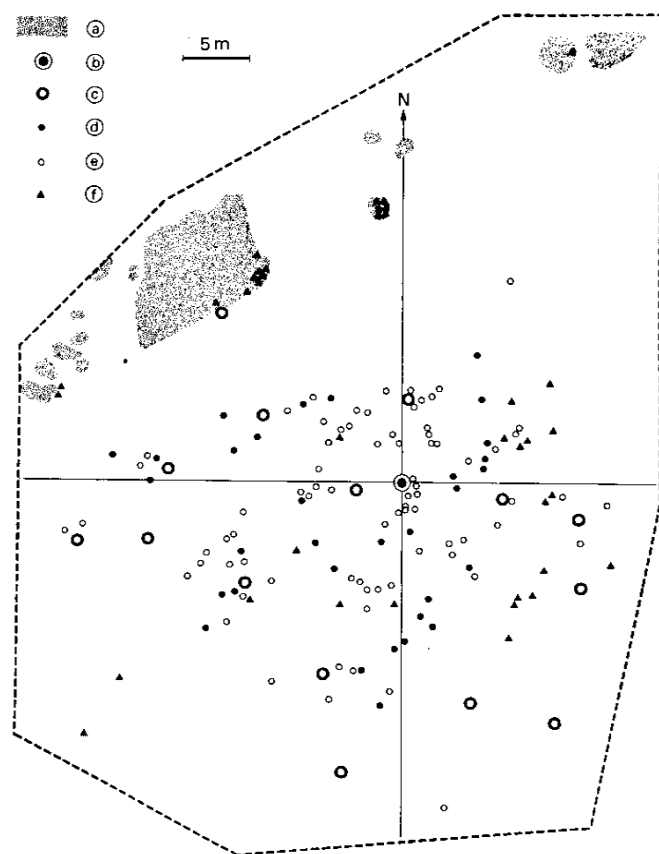


Fig. 2: Spatial distribution of finding sites recorded for a particular colony of *Cataglyphis bicolor*. (a) *Quercus fruticosa*; (b) *Cataglyphis bicolor* colony; (c) colonies of *Messor semirufus*; (d) site of reject (location where a food item has been found but not collected by a searching *Cataglyphis* forager); (e) finding site (location where a dead *Messor* specimen has been found and collected by a *Cataglyphis* searcher); (f) licking site at *Quercus fruticosa* or *Artemisia scoparia*. 77 findings, 32 rejects, and 38 lickings have been sampled. For definition of «searchers» and «lickers» see Chapter II.3. [Platamon]

2. Nest Sites

It is already the distribution of the nests themselves that can tell a lot about the foraging strategies of the colony. For instance, the distance to the nearest nest of an alien colony indicates the size of the foraging range which the nest in question might use exclusively. Depending on the kind of foraging employed by the species, this distance also reflects the extension of individual foraging ranges.

a) *Methods*. In all *Cataglyphis* species, the locations of the subterranean nests can easily be inferred from the positions of the entrance holes. As in *Cataglyphis bicolor* nest entrances are rather inconspicuous, the easiest way to find such nest is to check the area at that time of the day at which the ants are fully active. A searching ant met anywhere within the area was then rewarded with a piece of food whereupon it would immediately run back along a straight line to its nest. This procedure was repeated several times to locate the position of every nest within the study area.

A *Cataglyphis* colony can occupy several nests. The question which nests belong to the same colony is answered in two ways. The first method relies on the fact that there is a frequent exchange of individuals between the nests of a colony. Experienced (exterior) workers carry their nestmates (interior workers) from one site to another. By observing this frequent exchange, which only occurs during daytime, the connections between the nests can be established. Second, two workers taken from two different nests are placed together in a glass flask, or one is taken and freed in the entrance of another nest. *Cataglyphis* ants can readily distinguish, presumably by olfactory means, whether another ant belongs to the same colony. Workers of *Cataglyphis bicolor* that are forced to come close to one another do not tolerate members of an alien colony. In this way, observations of agonistic behaviour can be used to distinguish subdivisions of one colony from truly foreign colonies.

b) *Numbers and Densities of Nests*. The densities of nests vary dramatically between the Tunisian and Greek study site: There are 11.2 nests per ha in Tunisia, but nearly three times as many (31.0 nests per ha) in Greece (Fig. 1a,b). The areas investigated measured $1.5 \cdot 10^4 \text{ m}^2$ and $1.0 \cdot 10^4 \text{ m}^2$, respectively. The difference mentioned above is even more pronounced when one refers to the densities of colonies rather than nests. In Greece, the colonies consist nearly exclusively of one nest only. Thus the density of the nests corresponds with the density of the colonies. In Tunisia, however, a colony consists of up to 6 nests (Fig. 1b)⁶. Consequently, in Tunisia, colony density is much lower (2.6 colonies/ha) than nest density (11.2 nests/ha).

c) *Spacing of Nests*. Due to the lower density of nests, the average nearest-neighbour distance must be greater in Tunisia than in Greece. In August, this distance is $45 \pm 8 \text{ m}$ ($n = 14$). In Greece, adjacent nests are separated by only $11 \pm 1 \text{ m}$ ($n = 31$). These

⁶ Such a colony structure is conveniently termed «polydomous» (Wilson, 1971).

ues refer to nearest-neighbour distances between nests of alien colonies. The colonies are spaced fairly uniformly both in Greece and in Tunisia (Fig. 1).

Forager Force and Colony Size

Cataglyphis bicolor, the workers adopt a temporal polyethism with the oldest workers searching for food (see Schmid-Hempel, in prep.). As a consequence, only a fraction of the total number of workers can be observed above ground (exterior workers). Nevertheless, the total colony size can be estimated without destroying the nests if the proportion of foragers is known. Furthermore, for several reasons the period of time during which a worker performs its foraging tasks is of interest. This time sets an upper limit to the possibilities of acquiring foraging skill and gathering navigational information. Finally, the body size of the forager defines an important ecological parameter as far as food load capacities or interferences with co-existing competitors are concerned.

Methods. To estimate the forager force, records were taken of the number of ants leaving and entering the nest during a given period of time. Whenever an ant crossed a reference circle drawn around the nest entrance, this event was recorded as an *exit* (when the ant had left) or an *entry* (when the ant had returned). Some of the workers had previously been marked individually. Thus the number of foraging trips (exits and entries) made by individual ants could be determined. From this, the simple Lincoln-Petersen method (Southwood, 1976) revealed the total number of foragers. Of course, in Tunisia where a colony comprised several nests (Section III.2.b), all nests belonging to the same colony had to be sampled. A further method of estimating the number of foragers used in Greece was to record the numbers of exits and entries from the nest during the morning of activity in the morning in order to obtain a figure for the maximum excess of exits over entries. In this way, one obtains a minimum figure for the number of foragers. The percentage of the workers of a colony that were engaged in foraging was determined only at the Tunisian study site (Schmid-Hempel, in prep.). The result is assumed to be valid for the Greek area as well.

Head width taken at the ventral rim of the compound eyes was used as a measure of worker size. Head width is a convenient measure for ecological studies because it is directly related to the size of the mandibles which in turn determines the maximum size of prey that can be carried by a single forager. Also, it is a measurement that can be taken without too much difficulty on an intact live ant.

To estimate the life expectancies of foragers, a number of ants leaving the nest were captured at random and marked individually. On the following days, continuous records were taken of all individually marked ants. These records yielded the re-sighting probabilities of a worker of the initial sample. Due to a mathematical property – its

approximately exponential decay – this re-sighting curve represents the survival probabilities for a cohort⁷ of foragers.

b) *Number of Foragers and Size of Colony:* According to the Lincoln-index method, each nest is estimated to dispose of an average of 93 foragers (Tunisia). As several colonies belong to the same colony, the average forager force of a colony is 340 workers. In Greece, estimates lie between 200 and 300 foragers. Thus a somewhat greater forager force is present in a Tunisian as compared to a Greek colony, even though in the former this force is dispersed over several nest sites.

As described by Schmid-Hempel (in prep.), roughly 15 % of the total number of workers of a colony are actually foraging. According to this ratio, a colony comprises 2000–2500 workers in Tunisia and 1300–2000 workers in Greece.

c) *Body Size of Foragers.* The body sizes of the foragers differ markedly between the two study sites (Fig. 3). In Tunisia, head widths are much larger (2.62 ± 0.02 mm; $n = 304$) than in Greece (1.73 ± 0.05 ; $n = 90$). At the Tunisian study site the species *Cataglyphis albicans* occurs sympatrically (head width 1.27 ± 0.01 ; $n = 141$; Schmid-Hempel, in prep.). As demonstrated in Fig. 3, the body sizes of the Greek *Cataglyphis bicolor* nicely fit in between the body sizes of *Cataglyphis bicolor* and *Cataglyphis albicans* as measured at the Tunisian site.

d) *Number and «Biomass» of Foragers.* According to the difference in linear dimensions, the workers are markedly heavier in Tunisia than they are in Greece. At the former place the average fresh weight of a forager is 27.3 ± 0.6 mg ($n = 108$); at the latter it is 9.3 ± 0.8 mg ($n = 56$).

Combining the numbers of workers per nest with the densities of nests, one can estimate the total number of ants per unit area. For Tunisia, this procedure yields a number of about 7000 individuals per ha (190 g fresh weight per ha). The corresponding numbers for Greece are 46 500 individuals and 500 g fresh weight per ha. Obviously, the area in Greece is much more productive in terms of what *Cataglyphis* ants can exploit than the area in Tunisia.

e) *Life Duration of Foragers.* The numbers of foragers that have been marked individually at a particular day decline rapidly and in very much the same way at both study sites (Fig. 4). The rate of decay follows fairly well a negative exponential function as outlined by Schmid-Hempel (in prep.), these re-sighting frequencies indeed represent the survival probabilities of a forager cohort. Hence, the life durations of the foragers coincide at both study sites. Life expectancies were calculated to be 6 days.

⁷ A cohort denotes a group of individuals which enter a particular period of life at the same time. In human populations this may refer to individuals which are born on the same day. In the present case, a cohort denotes workers which shift from attending the interior tasks to foraging on the same day.

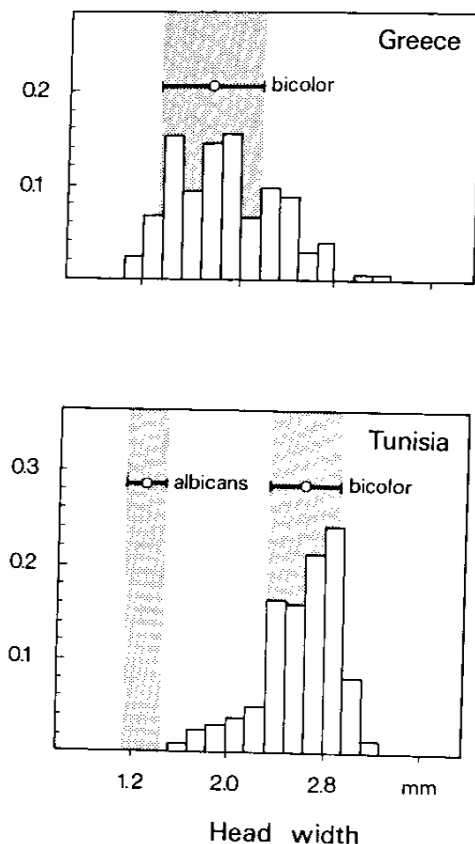


Fig. 3: Distribution of head widths of foragers (relative frequencies) measured in Greece (upper diagram, $N = 90$) and Tunisia (lower diagram, $N = 304$). Dot and horizontal bars indicate mean and standard deviation, respectively. The smaller species *Cataglyphis albicans* co-exists with *Cataglyphis bicolor* in Tunisia. The average head width of foragers in Tunisia (2.62 ± 0.02 mm S.E.) is larger than that at the Greek site (1.73 ± 0.05 mm S.E.; t-test, $p < 0.001$).

Cataglyphis ants attend to the foraging tasks at the end of their lifetimes (see Schmid-Hempel, in prep.). This is in agreement with results of histological studies derived independently (Fig. 5). The internal organs investigated – fat bodies, ovarioles and salivary glands – decrease in size in workers sampled in the following sequence: interior workers taken from the nest chambers – interior workers carried by foragers above ground – diggers – foragers.

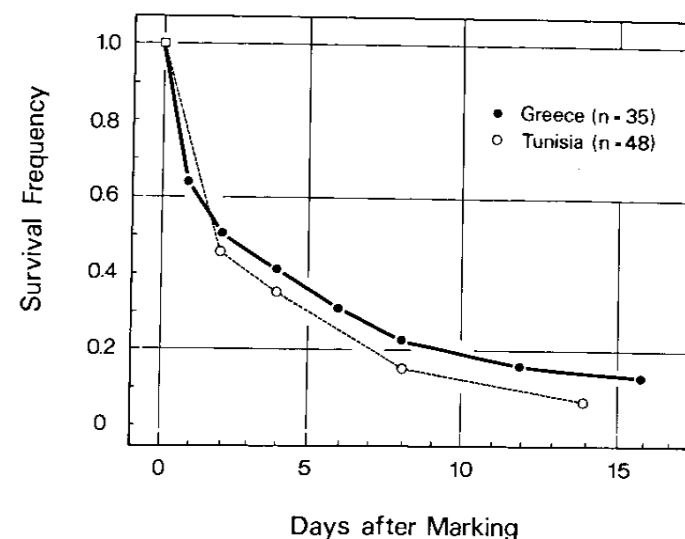


Fig. 4: Survival probabilities for a cohort of foragers. Each dot represents the number relative to the initial sample size of ants re-sighted on a particular day.

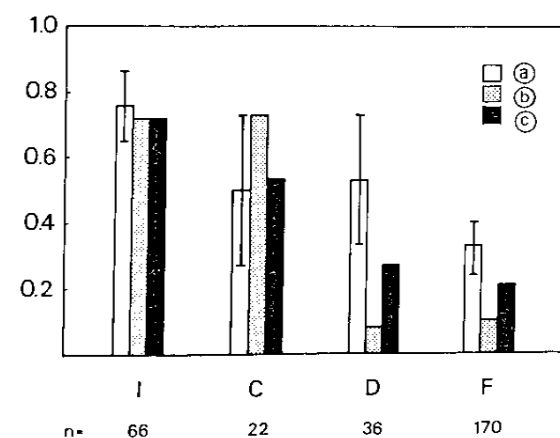


Fig. 5: Developmental stages of ovaries (a), fat body (b), and hypopharyngeal glands (c) in inside workers (repletes) taken from the colony (I), inside workers carried by foragers to other nests (C), diggers (D), and foragers (F) of *Cataglyphis bicolor*. For each of these organs a threshold value is defined anatomically above which the organ is regarded as fully developed (compare Weyer, 1927; Otto, 1958; Kirchner, 1964). The ordinate represents the number of specimens with well-developed organs divided by the total number (n) of ants investigated. Standard deviations are given in a. [Maharès]

4. Temporal Distribution of Foraging Activity

In foraging ecology, important questions relate to the time of day and night at which animals are searching for food. In addition, navigational strategies involved in foraging crucially depend on what time of day or night foraging takes place. For example, the use of the sun or the pattern of polarized light is only feasible for diurnal animals. Furthermore, if the animal uses celestial cues, the amount of time an ant spends outside the nest and searches for food indicates whether a time-compensated celestial compass is needed in determining homing direction.

a) *Methods.* As described earlier (Section III. 3.a), the numbers of ants leaving and returning to the nest were recorded whenever the ants crossed a reference circle (radius 2 m) drawn around the nest entrance. Data were collected over the entire daily foraging periods of different colonies (Figs. 6 and 8). In other cases, the numbers of leaving and

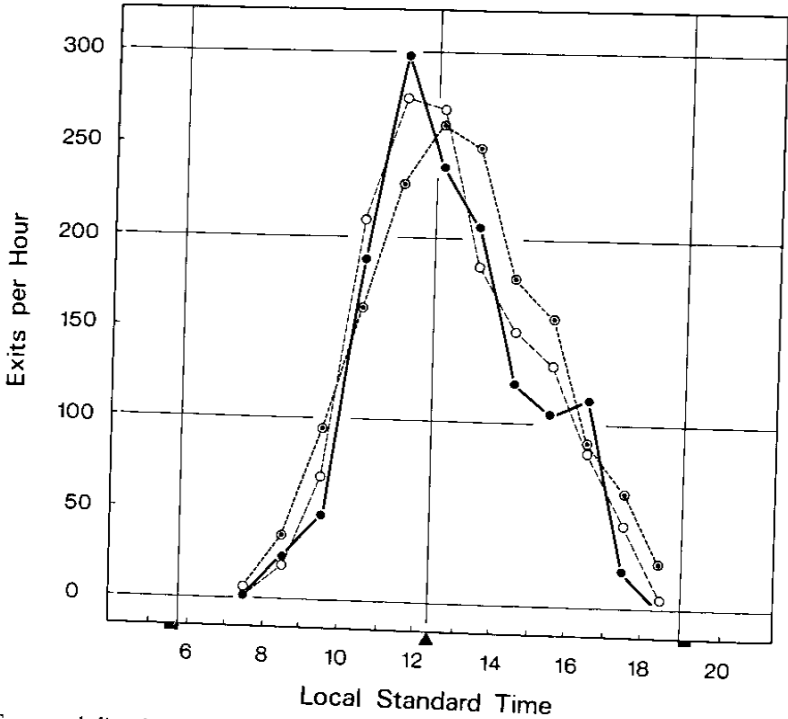


Fig. 6: Temporal distribution of foraging activity recorded at one nest on July 26, August 8, and August 14 (Tunisian study site). The numbers of foraging trips (exits) are recorded at a distance of 2 m from the nest entrance. The arrow marks local noon. The black bars at the abscissa indicate the times of sunrise and sunset as they occurred during the experimental period. [Maharès]

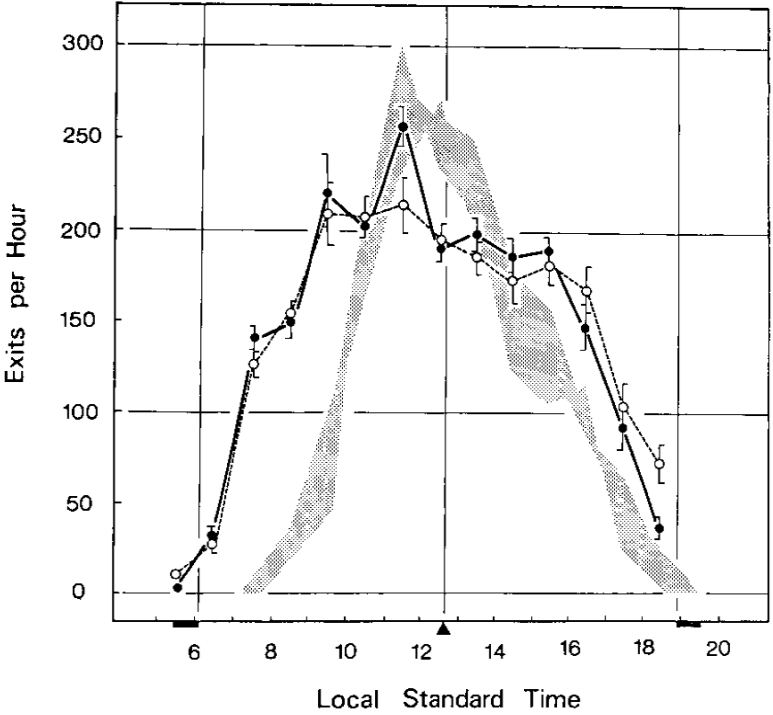


Fig. 7: Temporal distribution of foraging activity recorded at several nests of the Greek study site. Mean values and standard errors are given for two years (August) (solid and dashed line). The grey area indicates the corresponding distribution obtained at the Tunisian study site (for detailed data see Fig. 6). At the abscissa local noon and times of sunrise and sunset are marked by the arrow and the black bars, respectively. [Platamon as compared to Maharès]

returning ants were recorded several times per day, but over many days, and the data pooled thereafter (Fig. 7).

b) *Colony Activity.* At both study sites, *Cataglyphis bicolor* is a truly diurnal forager. Whenever records are taken, the numbers of exits per hour rise steeply in the morning and peak well before local noon. Correspondingly, the number of exits exceeds the number of entries during the morning hours, but this surplus vanishes before noon (Fig. 8). This indicates that most ants are searching outside the nest during the morning hours. However, the length of the daily activity period is slightly different at the two study sites. In Greece, the ants start earlier in the morning and finish later in the afternoon than in Tunisia. Thus, at the latter site, the activity curves peak more sharply than in

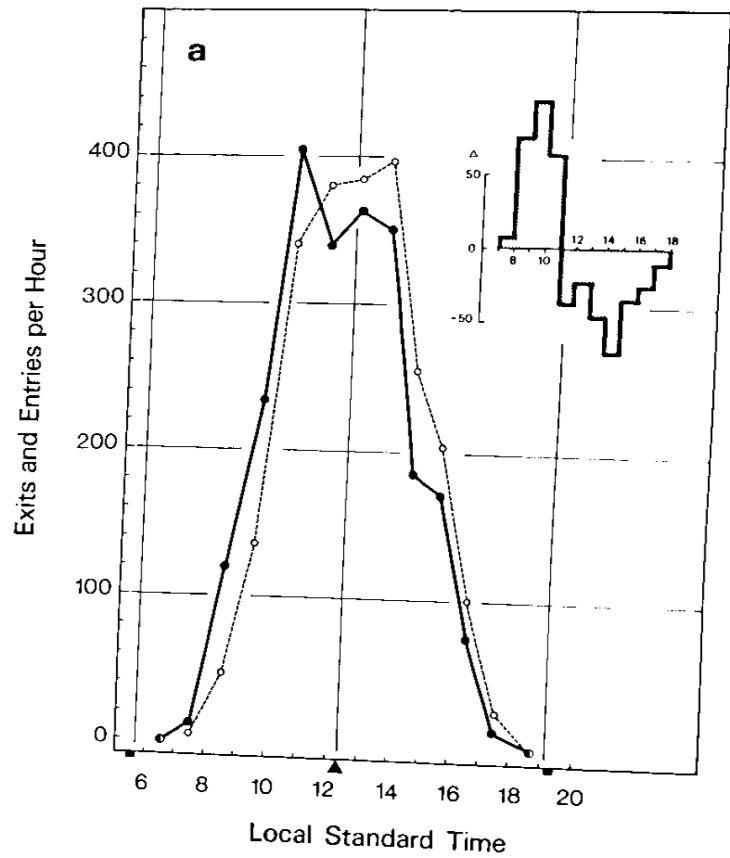


Fig. 8a

Fig. 8: Temporal distribution of foraging activity (outward and return trips) at two nests, *a* and *b* (August). The total number of outward trips (*exits*, ●) and return trips (*entries*, ○) is recorded at a distance of 2 m from the nest entrance. The *insets* depict the differences Δ between the numbers of exits and entries. In *b*, additionally, the frequency of exits is given for November (■). [Marrès]

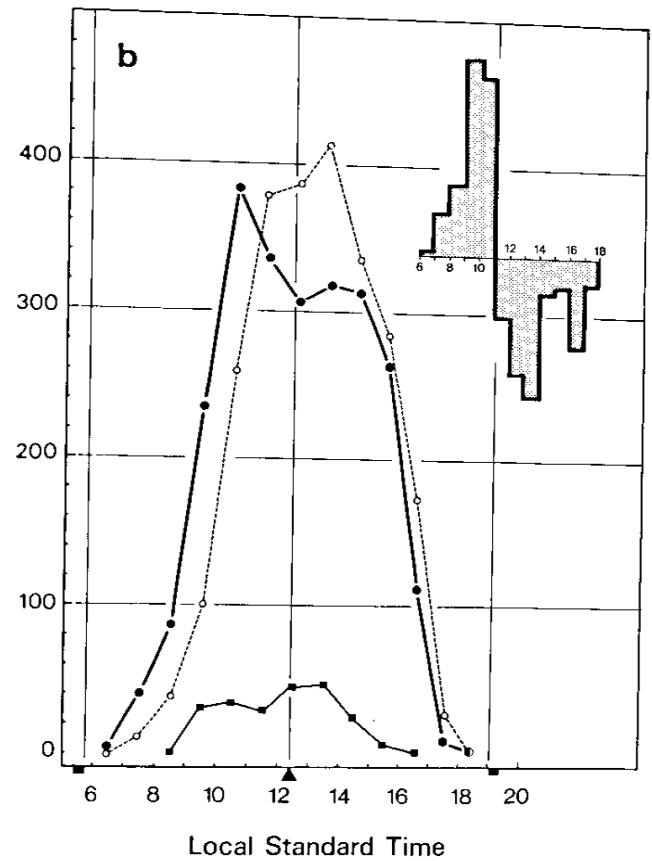


Fig. 8b

Greece (Figs. 6 and 7). On the average, the widths of the activity curves (numbers of exits) taken at half the maximum are 5.2 ± 1.1 hours ($n = 5$) in Tunisia, but 9.4 ± 1.6 hours ($n = 5$) in Greece (t -test, $p < 0.01$).

Individual Activities. The daily activity pattern is determined by the number of foragers active at any one time, and the number of runs these foragers perform per day. By observing the activities of individually marked ants, one can assess the relative importance of these two factors.

The whole day long, individual foragers leave and return to the nest repeatedly. The number of exits of any particular ant follows the background activity of the whole colony, e.g. most foraging runs start in the morning. Nevertheless, at the two study sites the individual foraging schedules follow clearly distinct patterns (Tab. 2). First, in Greece the searchers perform twice as many runs per day than in Tunisia. On the other hand, the duration of the runs is much shorter in the Greek foragers. Surprisingly, these figures coincide in successful and unsuccessful searchers. As can be deduced from the Greek records, lickens stay outside the nest for longer periods of time than searchers do (see also Harkness, 1977, 1979).

Another parameter characterizing individual time schedules is the temporal separation between successive runs. The time an individual stays inside the nest before it leaves again is much shorter in Greece than it is in Tunisia (Tab. 2). Despite these differences, the total amount of time an individual searcher spends foraging outside the nest each day is nearly the same at both study sites. On the whole, the individual ants exhibit rather different temporal foraging patterns in Greece and Tunisia, but the total amount of time allocated to foraging does not vary. It is kept constant at about 200 min per day (Tab. 2).

Table 2: A comparison of various parameters which characterize the foraging behaviour of individual ants, *Cataglyphis bicolor*. Data about *run durations* include those of successful and unsuccessful foraging trips. *Nest time* is the time an individual ant stays inside the nest between subsequent runs; *total-out time* is the sum of the time a forager is searching for food during a whole day. In Greece, this latter figure is calculated by multiplying the average number of runs/day/ant (first row) by the average duration of the runs (second row).

	Greece			Tunisia			T-Test
	\bar{x}	$s_{\bar{x}}$	N	\bar{x}	$s_{\bar{x}}$	N	
Runs/day/ant	9.5	1.5	24	4.2	0.3	52	$p > 0.0001$
Run duration (min)	19.0	1.2	165	52.9	3.9	86	$p > 0.0001$
Nest time (min)	7.5	1.2	67	47.5	7.7	49	$p > 0.0001$
Total-out time (min)	180.5	30.7	24	216.5	14.2	27	n.s.

5. Spatial Distribution of Foraging Activity

How are the spatial foraging patterns related to the spatial food availability? This is a fundamental question in foraging ecology. It has most recently been treated in a seminal paper by Hoelldobler and Lumsden (1980). In this investigation, we do not set out to inquire about how well *Cataglyphis bicolor* has adapted its foraging strategy to the spatial characteristics (patchiness, predictability, etc.) of its food distribution, neither will we engage in theoretical modelling. What we try to provide are experimental data about spatial extension and temporal stability of the foraging ranges of individual ants,

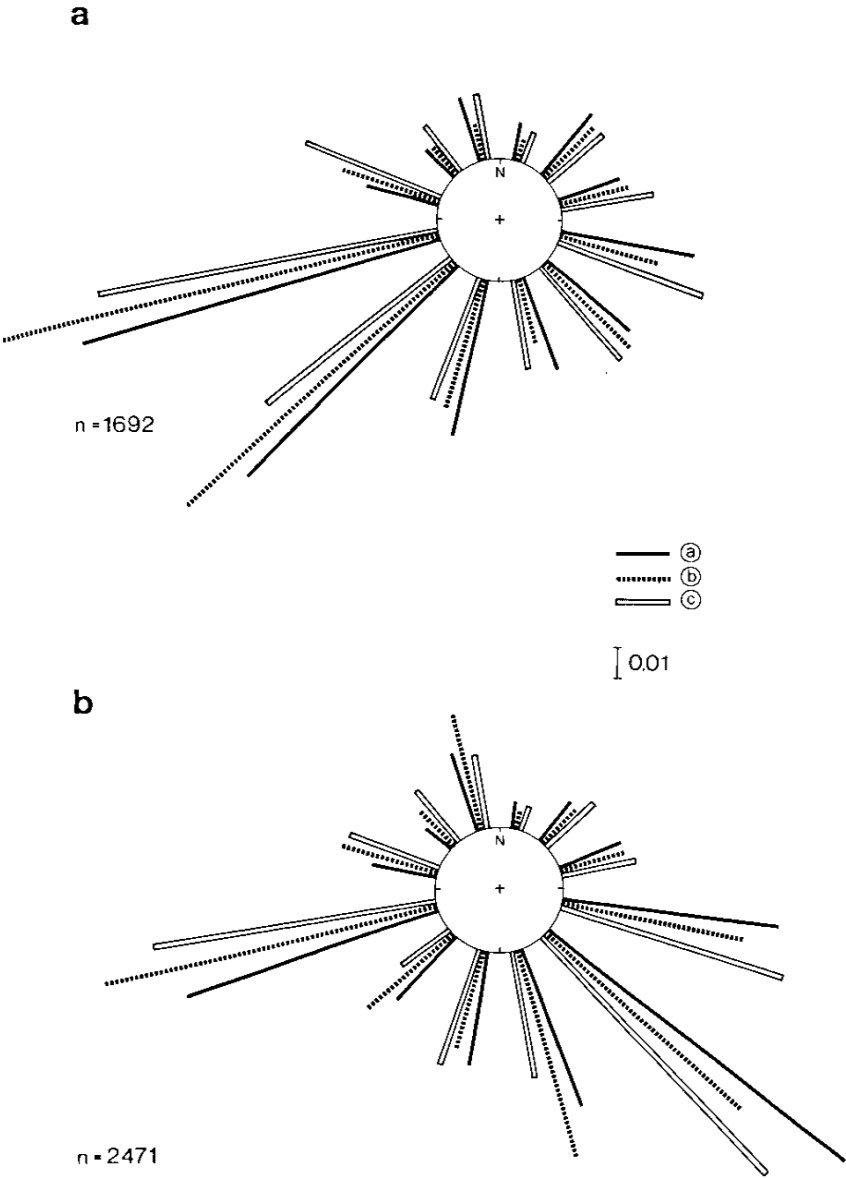


Fig. 9: Azimuthal distribution of foraging activity (relative frequencies) at the same nest on July 28 (top) and August 14 (bottom). (a) ants leaving the nest, (b) ants returning with loads, (c) ants returning without loads. Neither of the distributions is random (Rayleigh-test, $p < 0.001$; Batschelet, 1981). [Maharès]

and how the foraging ground of the whole colony is partitioned among individual ants. An answer to these questions is of major interest for studies on insect navigation. As an example, the spatial layout of a forager's activity provides the necessary background for judging about how familiar an individual ant is with its search area. If an ant frequently returns to the same area, any navigational system is favoured that relies on landmark cues.

Methods. Individually marked ants were followed during consecutive foraging trips. In Tunisia, a 3m-square grid was painted on the desert ground to facilitate the recordings of the foraging movements. Runs were recorded on scaled paper, and «fixes» (see Weems and Lee, 1958) were taken every 15 sec. In Greece, the observer recorded successive positions of the ants by placing numbered labels on the ground and later mapping the positions of the labels (see Section II.3).

In the following, the spatial distribution of foraging activity is expressed in terms of the spatial distribution of search density. Records of search density are obtained by counting the numbers of fixes (time marks) per unit area. The Greek data refer to average numbers calculated over a period of four years, but all taken in August. In Tunisia, all data were collected in August 1981.

For measuring the circular (azimuthal) distribution of the foraging activity of a whole nest, the reference circle drawn around the nest (radius 2 m) was divided into 12 sectors, each 30° wide. The sectors were marked with small sticks.

Azimuthal Distribution. Even though foragers leave the nest in all directions (Fig. 9), the frequency distribution around the nest is rarely uniform. In general, some directions have more movements than others. Over a period of time, the peaks can change their positions relative to the points of the compass. This suggests that the colony is able to adjust its spatial activity pattern according to the distribution of more profitable food resources. For example, in Tunisia, nests near household refuse dumps of the nearby village exhibit pronounced peaks pointing towards such sites. Similar peaks can also be produced experimentally by offering bait towards such sites. Similar peaks can also be observed in the circular distributions of exits and entries are very similar, the individual ants seem to be bound to particular sectors of the whole foraging range of the colony.

Radial Distribution. Fig. 10 shows how search density varies with increasing distance from the nest. It is instantly apparent that the radial search profiles follow the same general pattern at both study sites, but in Greece the overall search area of the colony is much more concentrated around the nest than it is in Tunisia. The area comprising 90 % of the search density is defined by a circle whose radius is $r = 13.5$ m in Greece, but more than twice as large ($r = 32.5$ m) in Tunisia. Hence, in North Africa foragers of *Cataglyphis bicolor* search within an area that is almost six times as large as the corresponding area in Greece. Furthermore, the average path length of a foraging trip (recorded until the ant has found prey or until it returns unsuccessfully to

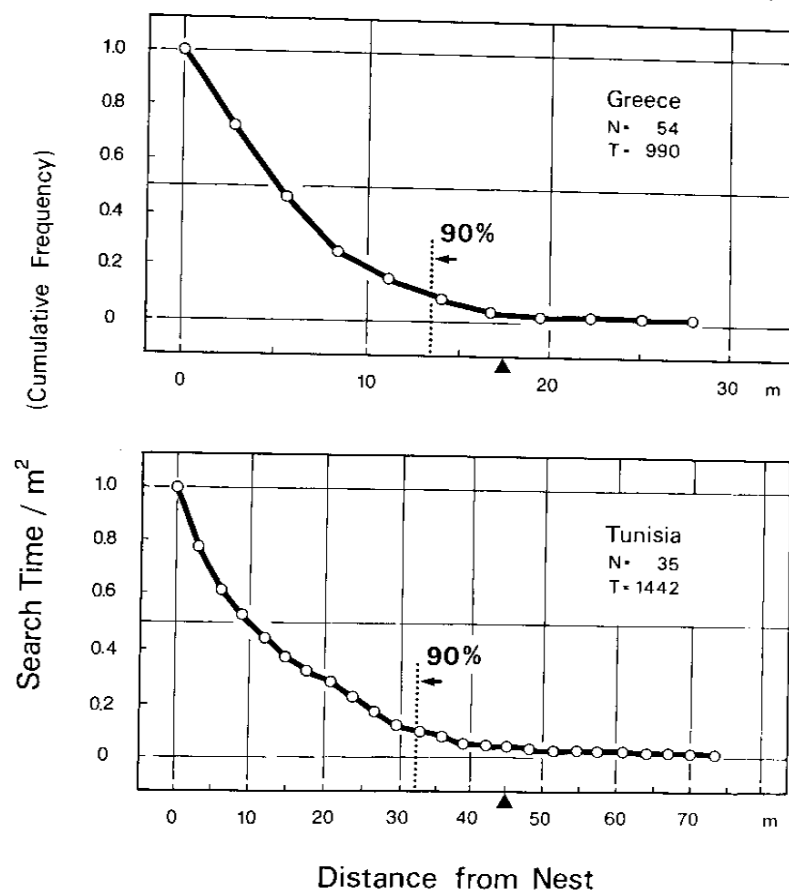


Fig. 10: Spatial distribution of foraging activity (cumulative frequency of search density) with respect to distance from the nest. The curves are the averages of N observed foraging runs of different animals that together lasted for T minutes. The dotted lines denote the distances up to which 90 % of the total amount of search density is located. Triangles indicate the average nearest-neighbour distance between nests of alien colonies.

the nest), is significantly larger in Tunisia than it is in Greece. At the former site, foragers cover an average path length of 103 m during each run. The corresponding number for Greece is 57 m. The former number has been obtained by direct measurements of individual foraging paths; the latter has been calculated by multiplying the average duration of a foraging run (Tab. 2) by the average foraging speed (3 m/min). Almost the same figure was obtained by adding the distances between successive 10 second fixes

from the numbers given above, the average path length of all foragers of a colony per unit area can be inferred. This was done by multiplying the average pathlength by the number of runs per forager per day (Tab. 2) and the number of foragers per nest (Section III.3.b), and then dividing this result by the foraging range covered (Fig. 10: 73 m² in Greece, 3318 m² in Tunisia). For a Greek colony, this calculation yields 65 m of search path per m² and day. In Tunisia, the corresponding number is considerably lower (13 m/m²/day/colony).

Distribution of Finds and Rejects. By following individual ants during their foraging runs, the locations where an ant takes a food item (*finds*) and then walks straight back to the nest can readily be recorded. However, the ants do not take every food item they encounter. If an ant investigates a food item with its antennae, but finally does not grasp the item but continues its search, this encounter is scored a *reject*. Rejection of food items by individual foragers can be due to «task» or «food fidelity» (see Rissing, 1981 a). On the average, one reject per two finds occurs. The distribution of these events – finds and rejects – follows fairly well the distribution of the search density given above (Fig. 11). Thus, the foragers remove the food items more or less according to the search time applied per unit area.

Overlap of Foraging Ranges of Nests. Comparing the spatial separation of the nests (Section III.2.b) with the search area of an average colony (Section III.5.c, Fig. 10), the same relation can be inferred for both study sites. The average nearest-neighbour

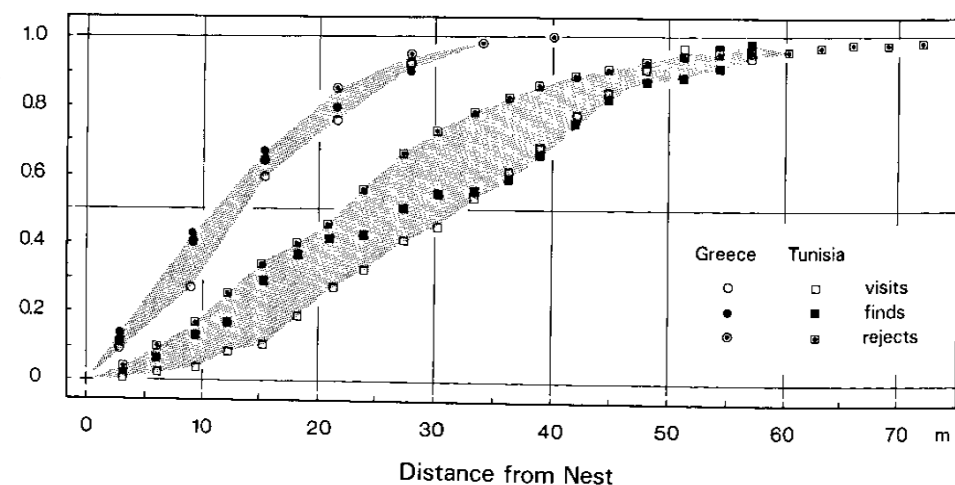


Fig. 11: Spatial distribution of foraging activity (searching density: visits) as well as finds and rejects of food items (cumulative frequencies). The distribution of foraging activity corresponds to that given in Fig. 10. Finds: N = 40; rejects: N = 79.

distance between any two particular nests corresponds with the radius of a circle within which all foragers of a colony spend 95 % of their total search time. In Greece, the nests are closer to one another, but the search areas of the colonies are much smaller than in Tunisia. As shown in Figs. 10 and 28, both parameters combine to such an extent that the degree of overlap between the search areas of adjacent colonies is nearly the same.

f) **Foraging Ranges of Individual Ants.** The circular distributions of the number of exits, as shown in Fig. 9 stimulate the question whether an individual ant leaves the nest indiscriminately in any one direction or whether it prefers a particular one. The observations of individually marked ants do in fact show that each individual ant invariably maintains a constant foraging bearing. This constancy is maintained over days and weeks and presumably extends over the whole lifetime of a forager (see also Harkness and Wehner, 1977, Schmid-Hempel, in prep.). Thus, in contrast to the temporal distribution of the foraging activities of individual ants (p. 22), the spatial distribution of

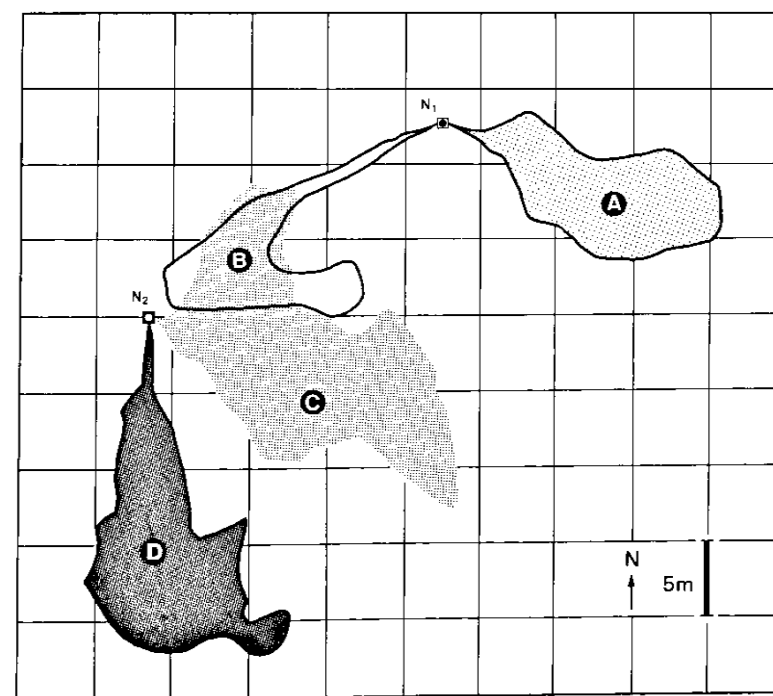


Fig. 12: Foraging ranges of 4 individually marked ants, A–D, belonging to two adjacent nests (N_1 , N_2). Foraging ranges have been mapped on the basis of 10–34 foraging paths recorded per ant over periods of 3–5 days. For detailed structure of the individual foraging ranges see Figs. 13–15. [Platamon]

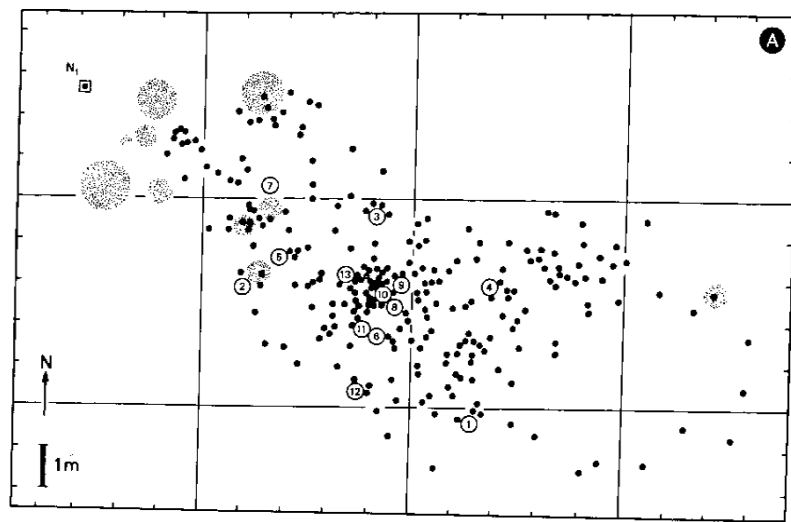


Fig. 13: The spatial layout of 13 foraging paths of an individually marked ant (see Fig. 12 A). Fixes of the ant's positions (small black dots) are taken every 30 sec. The sites where the ant has found food are indicated by open circles provided with the numbers of the foraging trips (e. g. ④ indicates the position of the finding site of the ant's 4th foraging trip). N_1 , nest entrance; light grey shading, plants of *Artemisia scoparia* (Compositae). [Platamon]

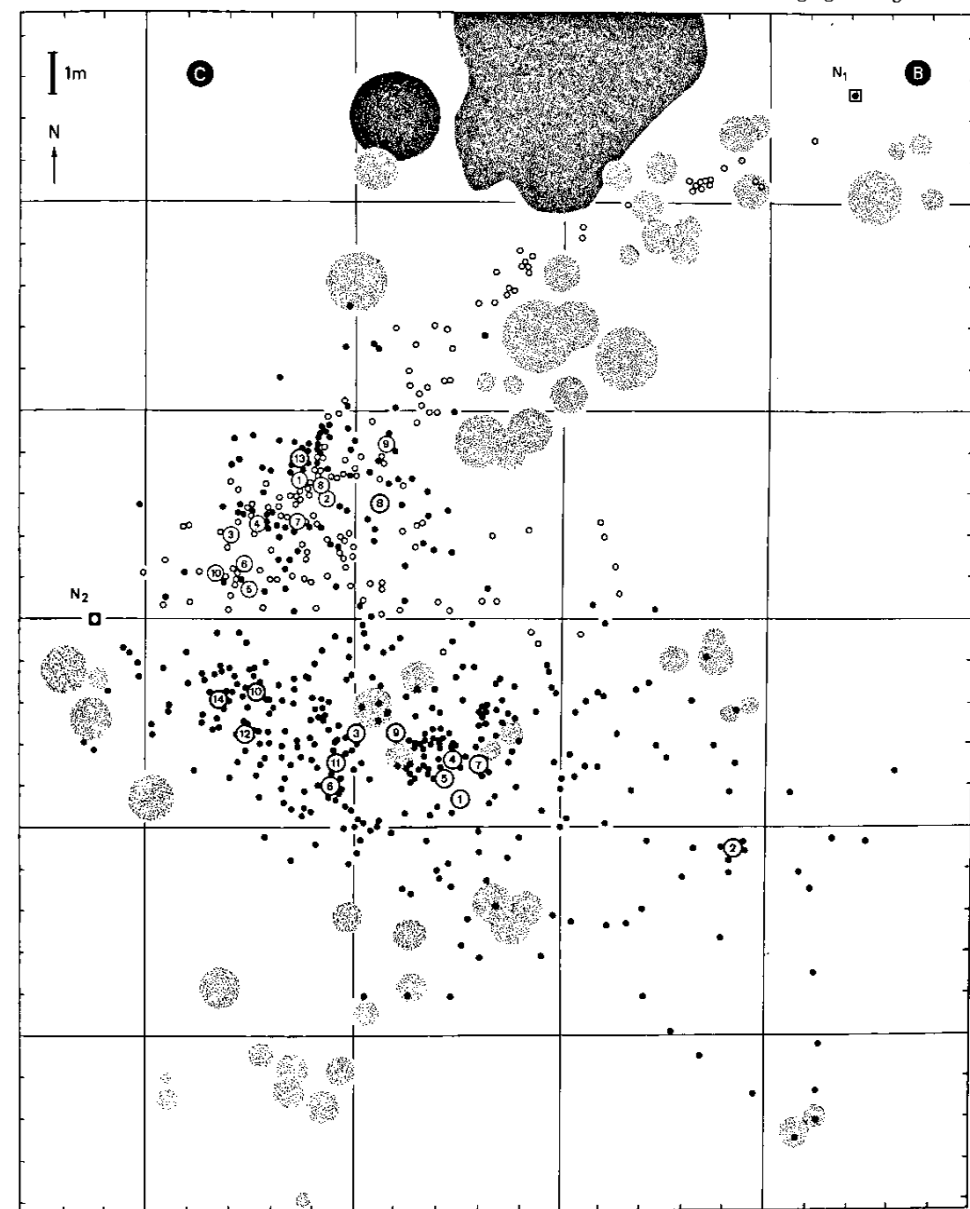


Fig. 14: The spatial layout of 10 (B) and 14 (C) foraging paths of two individually marked ants (see Fig. 12 B, C). Fixes of the ants' positions (small open circles refer to B, small filled circles refer to C) are taken every 30 sec. The sites where the ants have found food are indicated by the large open circles which are provided with the numbers of the foraging trips (B and C are differentiated by light and heavy symbols, respectively). N_1 , N_2 , nest entrances. Dark grey shading, bushes of *Quercus fruticosa* (Fagaceae). For further explanations see Fig. 13. [Platamon]

their activities does not reflect the behaviour of the colony as a whole. At the colony level, activity might be distributed uniformly over all points of the compass, but an individual ant restricts its activity to a small sector of the colony's activity range. Furthermore, during their entire foraging trips the foragers do not deviate much from their initial compass bearings (Figs. 12–16). As a consequence, the foraging range covered by an individual ant comprises only a minor fraction of the total foraging range of the colony. This kind of «sector fidelity» also accounts for the fact that there is a remarkable correspondence between the circular distributions of the numbers of exits and entries (Fig. 9). Each forager returns more or less within the same sector in the range of which it has left.

In addition, sector fidelity of individual foragers can be inferred from experiments where bait is offered in abundance at the same place and at the same time of the day for a number of successive days. Each day, the number of ants arriving increases more steeply than on the day before (Fig. 17). This is primarily due to an increase in the number of ants which arrive at the station rather than an increase in the frequency of visits of individual ants, since the time to complete a round-trip – a run to the nest and back to the bait – remains roughly constant after an individual ant has completed its

first few visits at the bait. Hence, the increase in the number of ants is easily explained by the assumption that a number of experienced ants already familiar with the position of the bait is joined every day by a certain number of newcomers. The number of newcomers arriving per day is determined by the rate at which these ants chance to

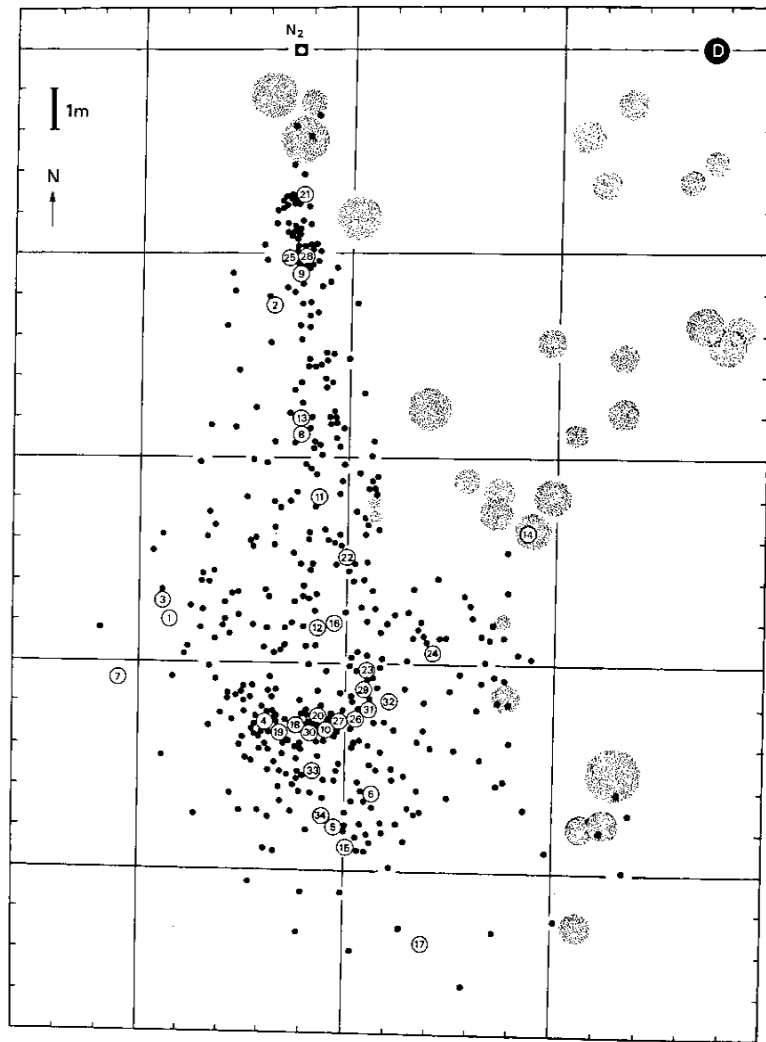


Fig. 15: The spatial layout of 34 foraging paths of an individually marked ant (see Fig. 12 D). For explanations see Fig. 13. [Platamon]

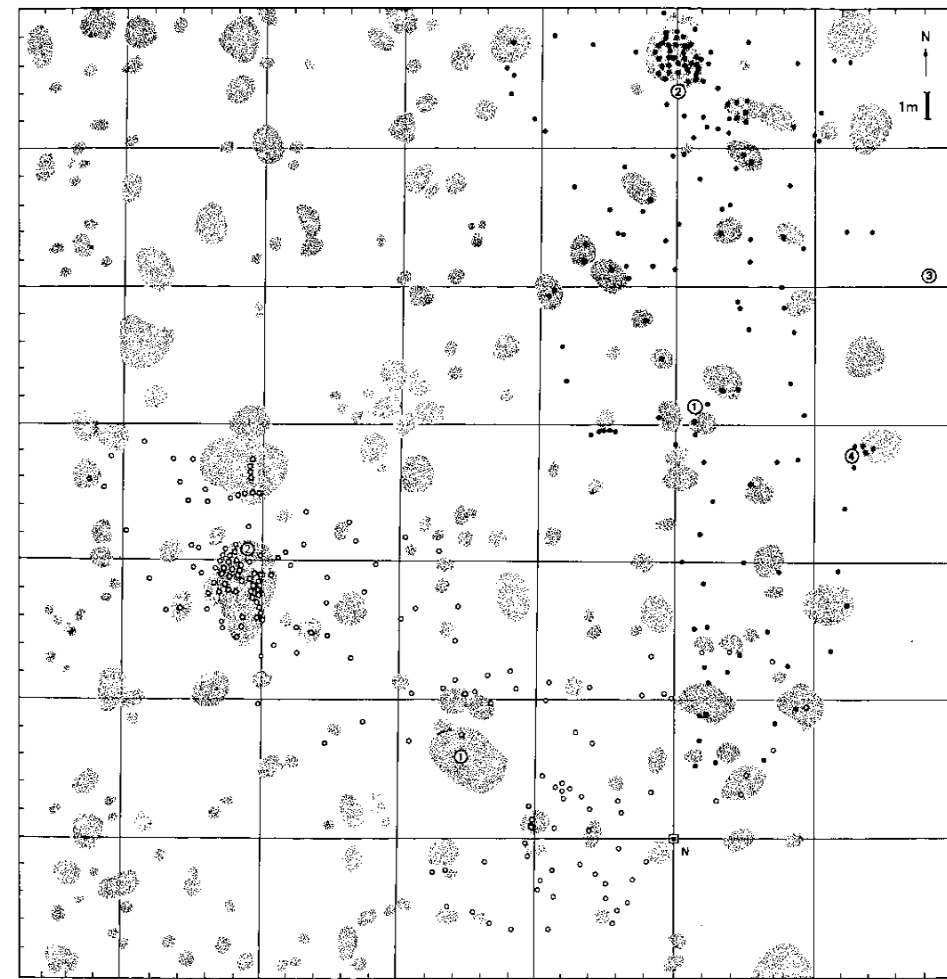


Fig. 16: The spatial layout of 2 and 4 foraging paths of two individually marked ants belonging to the same nest (■). Fixes of the ants' positions (small filled and open circles) are taken every 30 sec. The sites where the ants have found food are indicated by the large open circles which are provided with the numbers of the foraging trips (e. g. ② indicates the position of the finding site of the ant's 2nd foraging trip). Light grey shading, shrubs (see p. 5). [Maharès]

encounter this particular bait during their normal foraging runs. Calculations based on the spatial extent and spatial overlap of individual foraging ranges confirm this hypothesis (Schmid-Hempel in prep.).

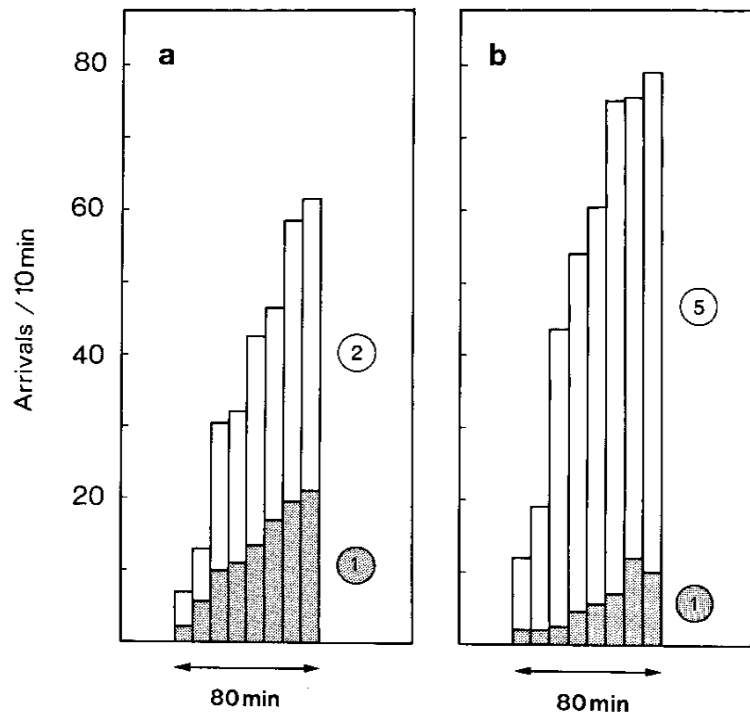


Fig. 17: Frequency of ants arriving at two feeding stations (*a*, *b*) on the first day after the stations were established (①) and on subsequent days – the second day at *a* (②), the fifth day at *b* (⑤). Food items were offered at the feeding station for 80 min each day, i. e. twice 80 min in *a* and five times 80 min in *b*. Figs. *a* and *b* refer to observations made at two different nests in two different years. [Platamon]

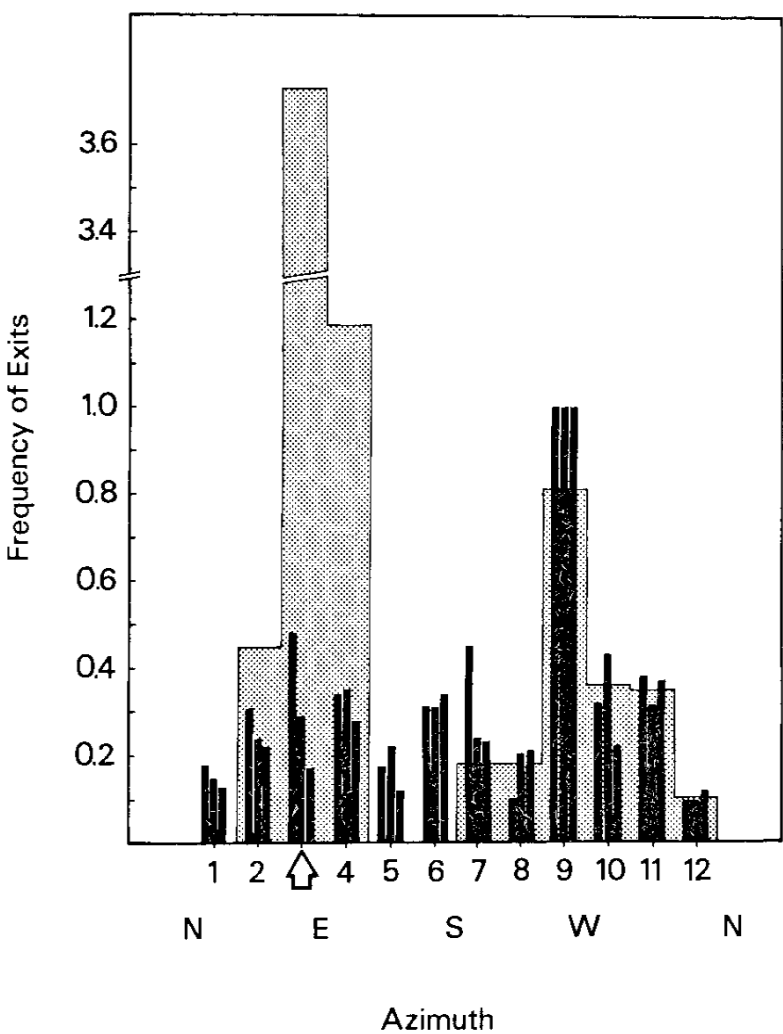


Fig. 18: Azimuthal distribution of foraging activity (frequency of exits) at one nest before (*black bars*) and after (*grey bars*) a feeding station was established in Sector 3 at a distance of 10 m from the nest. The *black bars* refer to the foraging activity as measured on 3 days within a period of 14 days. Frequencies *f* (exits/30°-sector/15 min) are given relative to the maximum frequency occurring at Sector 9 ($f_{\max} = 5.8; 11.0; 10.5$ exits/sector/15 min for each of the three days, respectively). Foraging activity after offering bait is given in terms of frequency at Sector 9 before offering bait. After the feeding station was installed in Sector 3, the frequency of exits increased at Sectors 2, 3, and 4, and decreased in the adjacent Sectors 1 and 5. For explanation see text. [Maharès]

Offering a bait in a particular direction leads to a pronounced peak in the frequency of exits pointing in that direction. In addition, the frequency of exits declines in the adjacent sectors (Fig. 18). These «inhibitory flanks» are due to foragers which usually attend to nearby directions but become trapped by the bait and subsequently leave the nest in the sectors pointing towards the food site. The previous analysis of individual search paths certainly shows that for any particular ant the spatial structure of the search path is strongly influenced by the preceding paths. This is not to say, however, that the ants always return to the very sites where they have been successful before. It only means that they concentrate their search efforts to individual foraging ranges (sectors that, in Tunisia, are some 50° wide and some 30 m long). Within these ranges, they often take the same route out from the nest and back to it, but the finding sites are distributed rather irregularly over their entire foraging

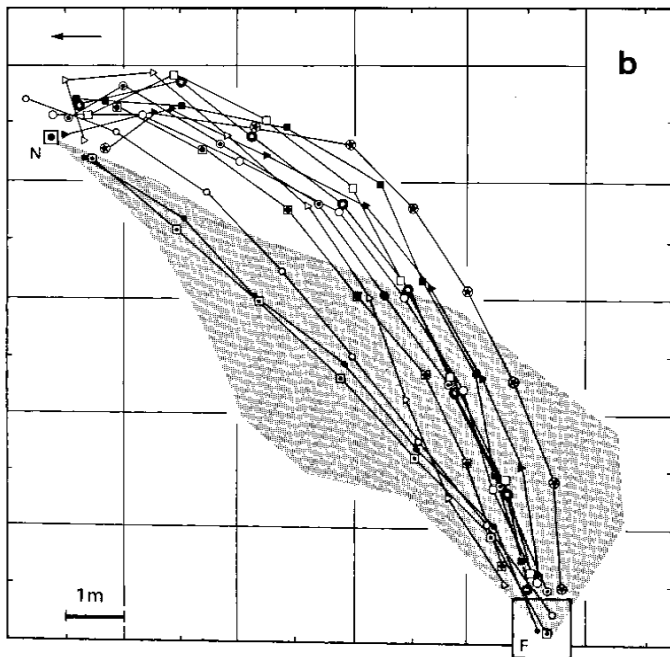
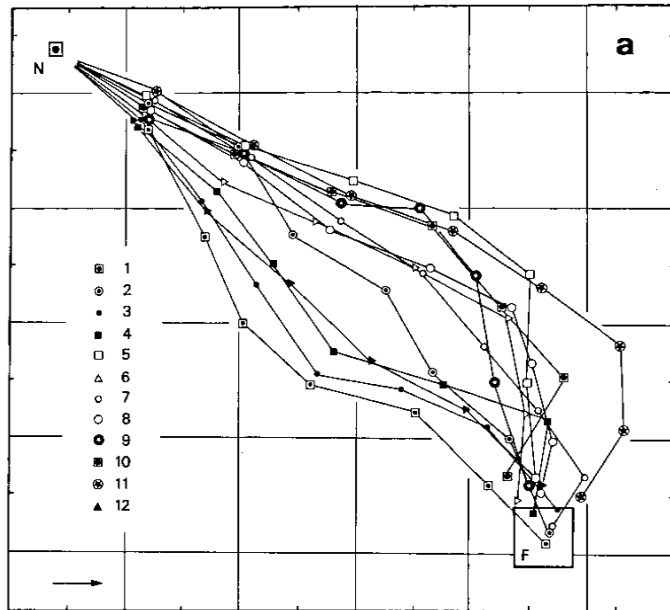


Fig. 19

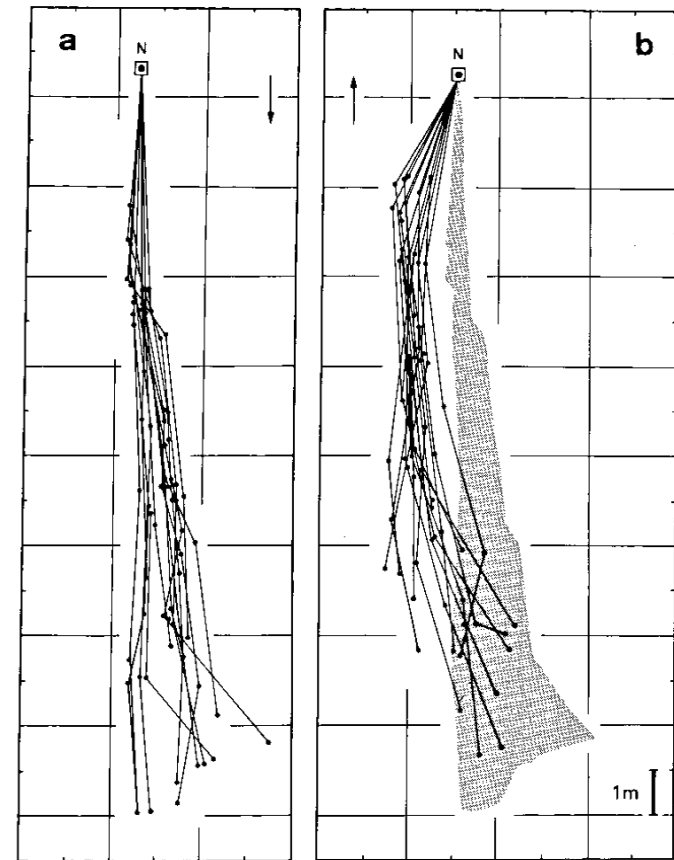


Fig. 20: Trajectories of 16 consecutive outward (a) and return trips (b) of an individually marked ant. Fixes of the ant's positions (●) are taken every 30 sec during the first and last 2 min of the outward and return trips. In b the area covered by the outward trips (a) is shown in grey. N, nest entrance. [Platamon]

◀ Fig. 19: Trajectories of 12 consecutive outward (a) and return trips (b) of an individually marked ant to an artificial feeding site. Fixes of the ant's positions (for symbols see inset) are taken every 10 sec. All outward and return trips were performed within 83 min. In b the area covered by the outward trips (a) is shown in grey. N, nest entrance; F, feeding site (1 m²). [Maharès]

ranges (see e.g. Figs. 13–15). This nicely underlines our previous statement that food items are nearly randomly distributed within the ants' spatial environment. As to the fine detail of the ant's foraging paths, two strategies can be distinguished: to search at the previous finding site first, or to pass by the previous finding site and search somewhere else. In both Tunisia and Greece, particular individuals seem to specialize in one of the two strategies. Finally, why are individual ants bound to spatially limited foraging ranges when the distribution of food is really unpredictable in space and time? An answer to this question might well have something to do with the constraints under which the ant's navigational system must work. This is the point to be considered next.

6. Navigational Strategies

As shown in the previous chapter individual foragers restrict their searching activities to small and distinct sections of their spatial environment. In the following, let us inquire in more detail about the spatial structure of individual foraging runs. How consistently do individual ants follow the same routes when leaving and returning to the nest, and how consistently do they return to places where they have been successful before? These are the topics to be considered first (Section III.6.a). As a next step in answering the question of how the ants find their way, successful foragers are displaced within their individual foraging ranges from one place to another, and their homing

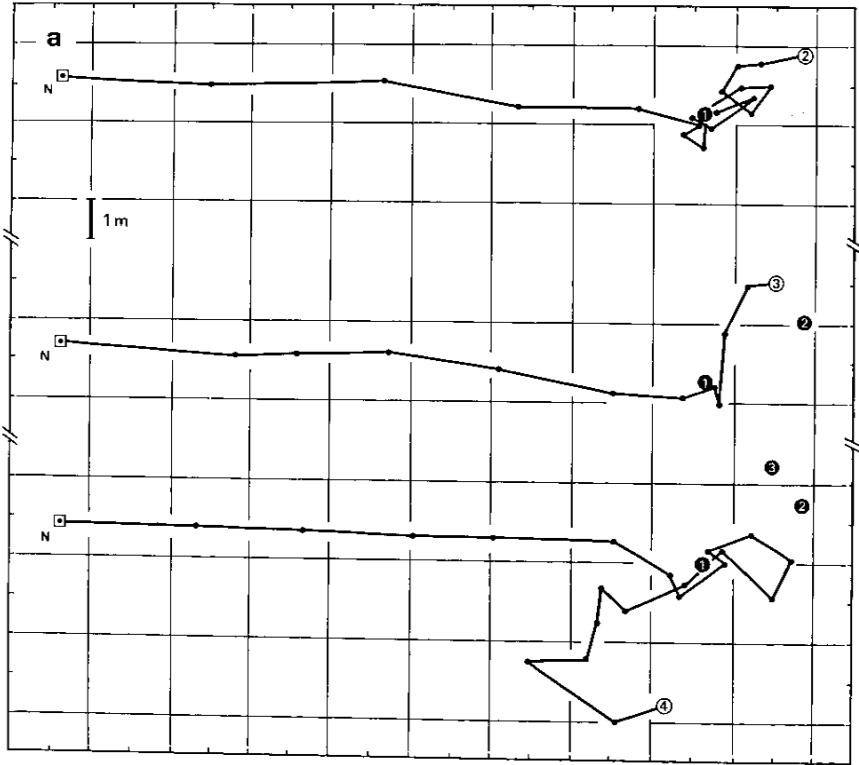


Fig. 21a

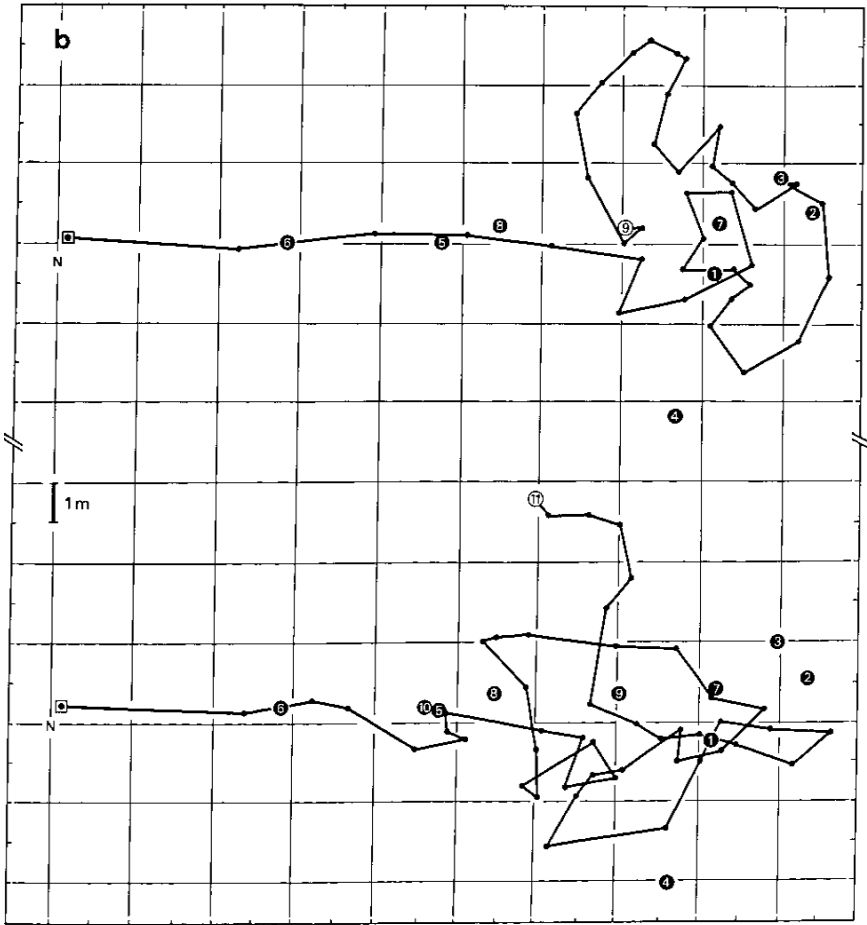


Fig. 21b

Fig. 21: Trajectories of foraging trips nos. 2, 3, 4 (a), 9 and 11 (b) of an individually marked ant. Fixes of the ant's positions (black dots) are taken every 30 sec. At the end of each trajectory the finding site is indicated by an open circle containing the number of the foraging trip. Large filled circles mark previous finding sites. Numbers refer to the numbers of the foraging trips recorded. N, nest entrance. [Platamon]

are recorded (Section III.6.b). Finally, the hypothesis about the ant's navigational strategy as derived from these displacement experiments is tested by exposing the ants to artificial landmark environments (Section III.6.c).

Spatial Structure of Individual Foraging Paths. In a structured environment where artificial landmarks such as small bushes or annual plants are available as navigational aids, individual foragers follow distinct routes when leaving the nest and returning to it. Often, the trajectories of the outward and return paths differ consistently (Figs. 19 and 20). Thus, the sequence of landmarks encountered by the returning ant is not just the reversed sequence experienced during the outward trip.

At larger distances from the nest, individual foragers vary considerably in how they allocate their search effort to certain localities within their foraging range. Some ants spend more time in searching at sites of previous rewards than others. Some restrict their search to limited areas, where they follow tortuous paths, others cover huge areas by following along straight trajectories. Individual foragers do not switch from one search pattern to the other, but maintain a given pattern throughout their lifetimes. What behavioural idiosyncrasies mean in terms of an optimum foraging strategy of the whole colony is discussed extensively by Schmid-Hempel (in prep.). With respect to the navigational aspects considered here, let us concentrate on the more consistent foraging patterns.

Examples are depicted in Figs. 21–23. In consecutive foraging trips, all three ants repeatedly search at localities where they have found food before. In the case of Fig. 21, the ant confines its searching activity to two locations, at least during a sequence of 11 foraging trips. In Figs. 22 and 23, the ant having been unsuccessful at the previous foraging site returns to an area where it had been successful farther back in the past. Obviously, a *Cataglyphis* ant is able to locate more than one finding site within its foraging range. Thus, it needs a map.

Landmark Routes. To unravel the nature of the ant's map, individually marked foragers are trained to an artificial food source located within their familiar foraging range. After they have run back and forth between nest and food source at least five times, they are displaced for short distances (35–85 % of the training distance), and in various directions. After release, their return paths are recorded.

What strikes us immediately when looking at the results (Fig. 24) is the fact that at the point of release (Nos. 1–8) the ants always choose the direction that would have led them to the nest (N) had they been released at the food source (F), but did not lead them from the place where they were in fact released (positions Nos. 1–8). Thus the ants do not walk straight home. This means nothing but that they do not use a map by which they can compute the direction towards home from any point of their foraging range. Instead, they adopt a dead reckoning (vector navigation) strategy relying on a compass and some means of measuring distances (Wehner, 1982 a). During a foraging

trip the ant records the direction and distance of each segment of its path and sums up all these unit vectors. The mean vector, reversed by 180° , leads directly back to the nest. As a consequence, pure vector navigation would guide the displaced ants to points marked by the tips of the white arrows. (A white vector is obtained by inverting the black vector leading from N to F and shifting it to a given point of release, marked by black dots at the centres of the circles indicate the mean positions where the ants stop searching for the nest. The radius of each circle represents the standard error (see Table 25 for method of determining the search point).

There is a marked difference in the homing behaviour of ants released at points Nos. 6, 7 and 8 and those released at points Nos. 2–5. In the former case, the ants stop searching where they would be expected to if they were using vector navigation (tips of white arrows). In the latter case, however, they do not stop at the points indicated by the home vector (tips of white arrows), but continue their straight homeward runs (dashed lines).

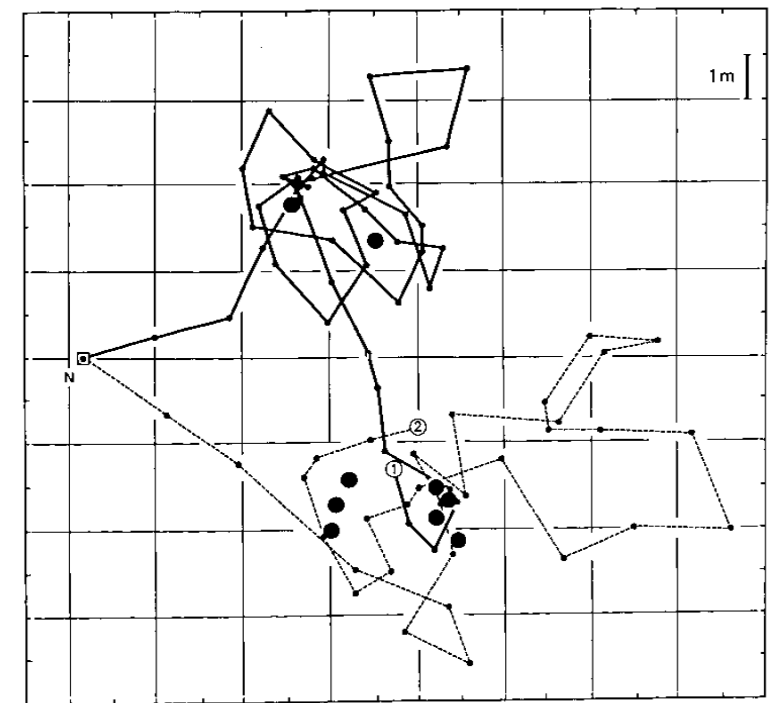


Fig. 22: Trajectories of two consecutive foraging trips of an individually marked ant. For details see Fig. 21. [Platamon]

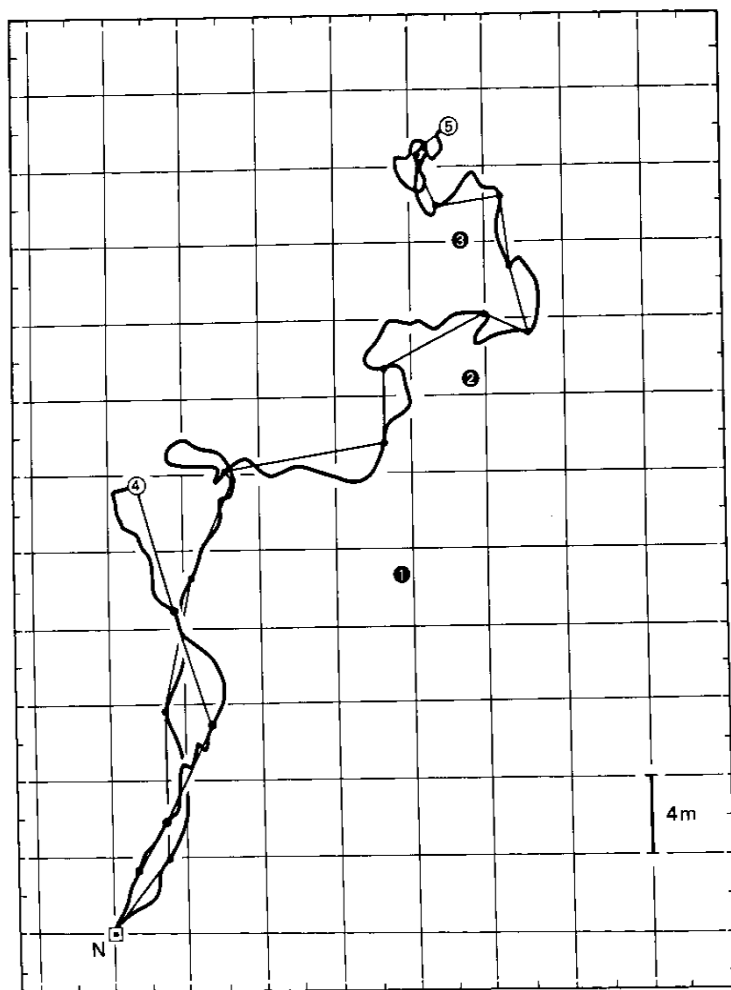


Fig. 23: Trajectories of two consecutive foraging trips of an individually marked ant. Fixes of the ant's positions (small black dots) are taken every 60 sec. For explanations see Fig. 21. [Maharès]

they are in fact very close to the nest. The additional information used to reach the nest in the latter case must have been derived from the familiar landmark panorama which the ants got to know during their former return runs from F to N. When the ants are released at points Nos. 2–5, vector navigation leads them close to the familiar landmark route F → N. However, when they are released at points Nos. 1, 6, 7 and 8, they finally arrive at positions (black dots) that lie outside this route. The landmarks surrounding

route F → N are visible even from the latter positions, but from there they appear in perspectives unfamiliar to the ants. The ants stop and start searching⁸. Obviously, they rely on a sequence of memory images characterizing the particular route F → N, and do not use a topographical map in which the positions of the landmarks are specified irrespective of the ant's own position. This hypothesis is tested in the following section by using artificial landmark panoramas.

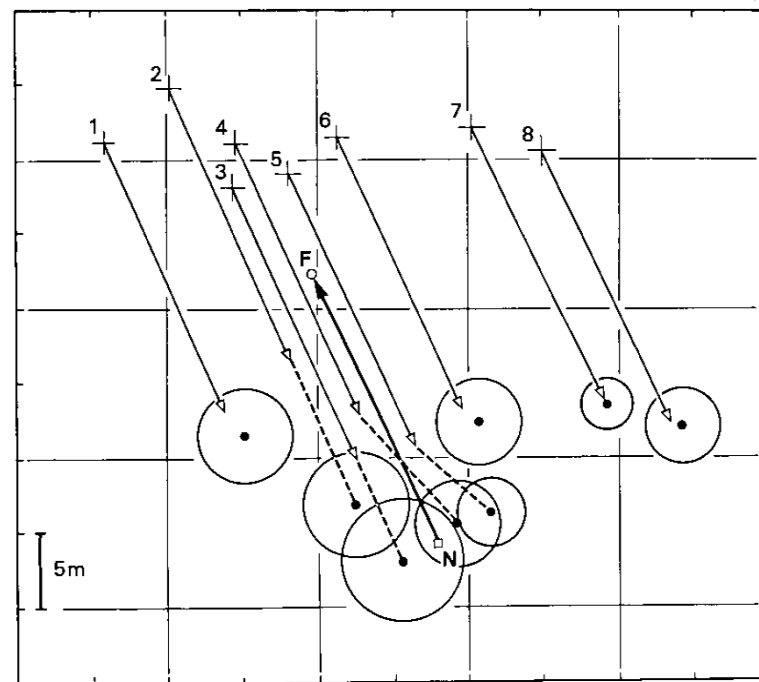


Fig. 24: Homing in ants which have been trained from the nest (N) to an artificial food source (f) and have then been displaced to different points of release (crosses, Nos. 1–8), $n = 74$. Black arrow, mean vector of the outward paths; white arrows, theoretical home vectors. If the homing ants relied exclusively on vector navigation they should stop walking along a straight line whenever they reach the locations marked by the tips of the white arrows. Black dots, mean location of the points where the ants start searching (end of straight homing path, for definition see Fig. 25). The circles drawn around the black dots indicate standard errors. The mean homing directions pointing from the starting points (crosses) to the searching points (black dots) have been recorded at a distance of 10 m from the start. Dashed lines, sections of the straight homing paths that cannot be accounted for by vector navigation, but are due to piloting along a familiar landmark route. [Maharès]

⁸ In the actual experiments, the ants were captured shortly after the search points had been determined. If they had been allowed to continue their searches, sooner or later they would have ended up at the nest due to a sensible backup system, their strategy of central place searching (Wehner and Srinivasan, 1981).

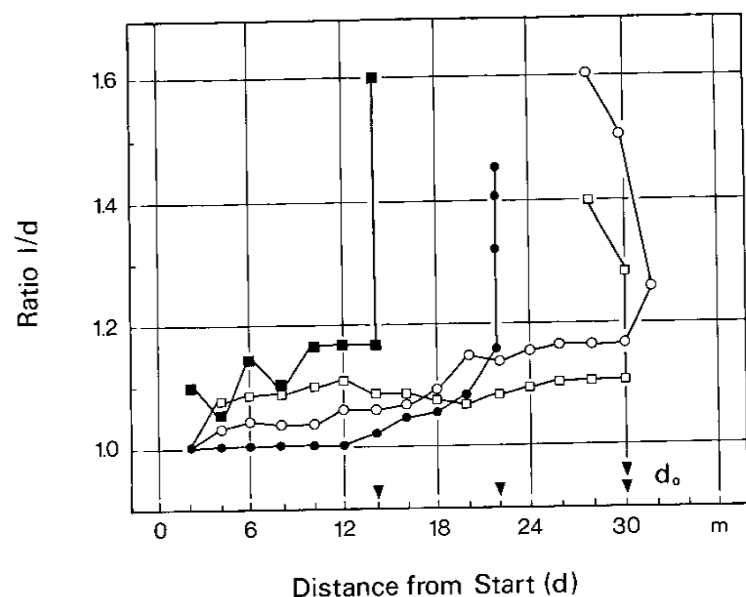


Fig. 25: Definition of distance d_0 (inverted black arrows) at which a homing ant starts searching, i.e., stops walking along a straight trajectory. Four examples are shown. l , path length actually travelled by the ant; d , distance from the start (point of release). For different distances d the ratio l/d has been calculated and plotted. $l/d = 1$ refers to a straight homing path. d_0 is defined as that value of d at which the ratio l/d rises steeply and consistently. [Maharès]

Memory Images. A colony of ants is displaced from its natural habitat to a vast open plain where the bare ground is completely devoid of any vegetation. Artificial landmark panoramas consisting of one, two, or more black cylinders are arranged around the entrance of the nest. After the foraging ants have become acquainted with their new spatial environment (training area) for one day, they are individually displaced to a third (test) area covered with a grid of white lines. This grid is used as a reference system in recording the ants' paths. In the test area the landmark cylinders are arranged either in the training configuration (control tests) or in modified configurations (critical tests). The present account refers only to experiments in which two cylinders are involved.

The ants are trained to a spot between the two cylindrical landmarks. During the test, they are exposed to four different landmark configurations: markers arranged at training distance (a) or half-training distance (b), markers half-training size arranged at half-training distance (c) or full training distance (d). It is only when the apparent sizes of the landmarks coincide with what the ants have experienced during training (Figs. 25a, 25b) that the ants search midway between the two markers. Under these conditions, the apparent size of each cylinder is 10° (height) \times 6° (width). When the landmarks

appear larger (Fig. 26 b) or smaller (Fig. 26 d) due to changes of either distance or size respectively, the ants get lost. Hence, they confound distance and size and rely exclusively on the size of the landmarks.

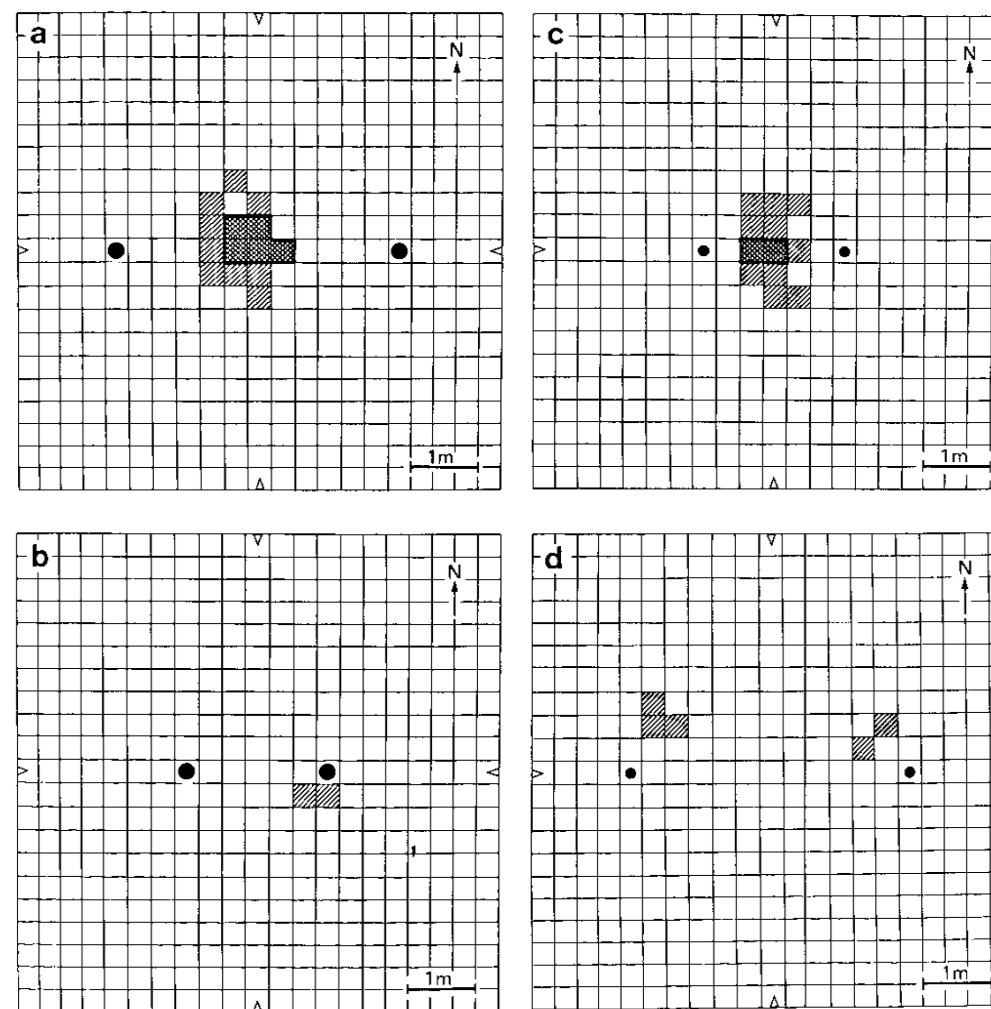


Fig. 26: Searching of *Cataglyphis bicolor* for the nest site. The nest site is marked by two cylindrical landmarks (height 38 cm, diameter 22 cm), positioned east and west of the nest entrance. a Control test: Sizes and distances of the markers coincide with those used during training, but the markers are transferred to the test area some hundred meters away from the training areas. b–d Tests: Sizes and distances of the markers varied with respect to the training situation. b Markers separated by half training distance. c Markers half training size separated by half training distance. d Markers half training size separated by training distance. The four white arrows point towards the position of the nest. In each figure, search densities are calculated on the basis of the total path length recorded for 7 ants for 5 min each. Cross-hatched, $> 70\%$ maximum search density; hatched, $< 70\% > 40\%$ of maximum search density.

on the two-dimensional panoramic image as seen from the nest entrance. This is in accord with the hypothesis derived at the end of the last section.

In the experiments just described, *Cataglyphis* adopts a new search strategy whenever the memory image does not coincide with the current image, that is when the landmarks, although appearing at the same azimuthal positions as during training, are either increased or decreased in size by no more than a factor of 2. Then, instead of searching the way between the markers, the ants search very close to either marker, running to and fro between them. In the case of Fig. 26 d where the size of each cylindrical landmark is decreased, they turn towards such a landmark when its dimensions are 3.7° (height) $\times 2.2^\circ$ (width), or even less.

In a second series of experiments (Fig. 27), two cylindrical landmarks are arranged in a way that they are separated by an azimuthal angle of 60° rather than 180° as seen from the entrance of the nest. Now, the landmark configuration has become ambiguous. Opposite to the nest entrance, there is another point at which the landmark panorama coincides with what the ants experience at the nest. The ambiguity can be resolved by referring either to distant landmarks or to celestial cues. Surprisingly, the ants do not resort to the latter possibility even though the ever blue sky vaulting over the desert provides conspicuous compass information. They do not use a celestial compass in order to decide whether the nest is north or south of the two landmarks. When the test area is far off the training area, so that the distant landmark panorama (maximal height 2.8°) bears no resemblance at all to that of the training area, the ants search indiscriminately at both points (Fig. 27 b). On the other hand, they are able to resolve the ambiguity if the training and test areas share a common skyline (Fig. 27 a). The main result drawn from these and many other experiments not described here is that in piloting themselves home the ants adopt a simple strategy of template matching. They try to match a panoramic memory image (template) with whatever current image they experience during homing. Apparently, they do not extract more generalized information from these landmark panoramas. This is nicely borne out by the experiments depicted in Fig. 26. There, the ants do not apply the seemingly simple rule that the nest is midway between two identical markers, irrespective of the sizes of the markers.

Further experiments have shown that the memory image is fixed with respect to a central system of coordinates. Usually, walking *Cataglyphis* ants keep the orientation of their heads, and thus their eyes, fixed with respect to both roll and pitch (see Wehner, 1982 a, Fig. 19, p. 45). Knowing the directions of view of the individual ommatidia, and the compass bearing of the ant, one can then define the regions of the eye onto which a given landmark is projected. If those parts of the eye are painted out, the ants are no longer able to use this landmark for navigation, irrespective of whatever other parts of the eye have been left open. The memory image seems to be defined in terms of central coordinates. Strictly speaking, this statement only holds with respect to movements about the roll and pitch axes. What remains as a really intriguing question is

whether the memory image is also fixed with respect to the dorsoventral (yaw) axis, or whether it can rotate inside the ant's head about this axis, i.e. parallel to the horizon.

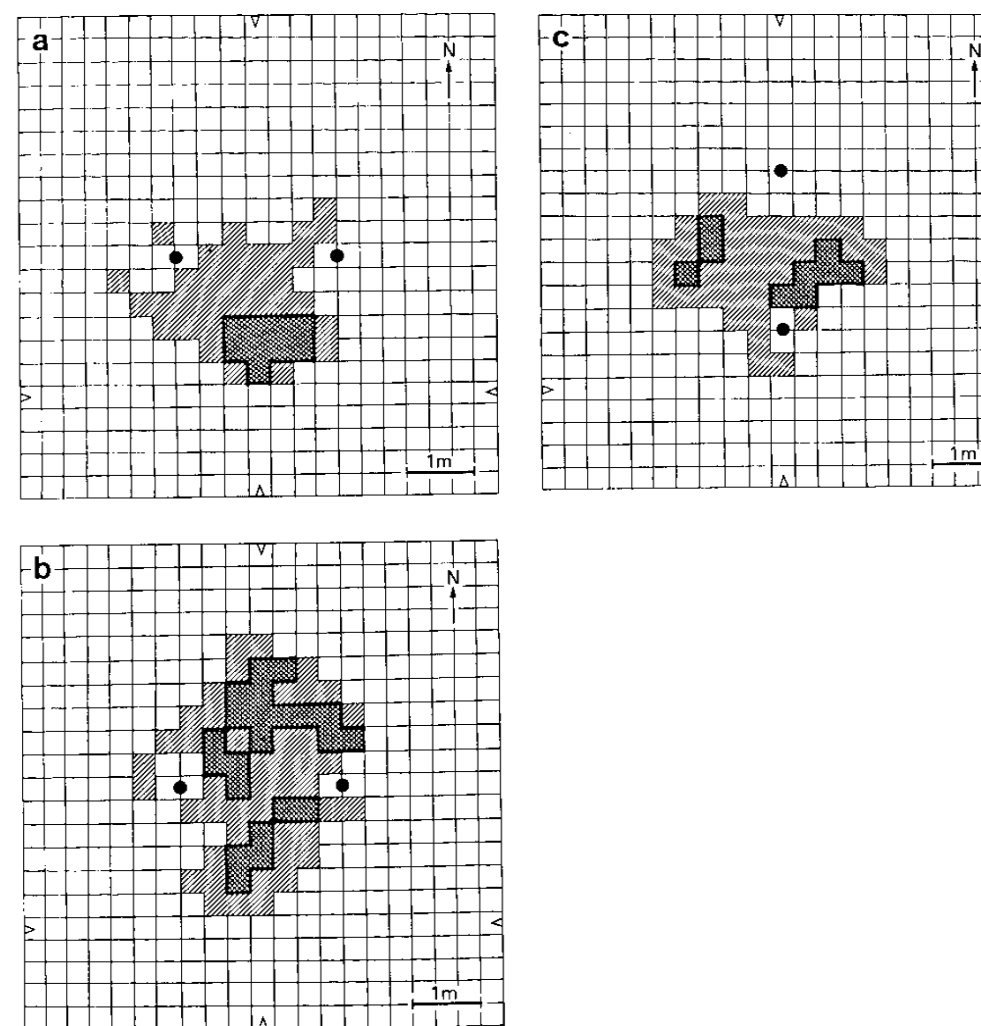


Fig. 27: Searching of *Cataglyphis bicolor* for the nest site. The nest site is marked by two cylindrical landmarks positioned at an azimuthal distance of 60° to the north of the nest entrance. The white arrows point towards the position of the nest. a Test area near to the training area so that the distant landmark panorama coincides in both cases. b Test area several hundred meters away from the training area: Skyline differs from that of training area. c Test area as in b but landmark configuration rotated by 90° . For definition of search density (cross hatched) see Fig. 26.

IV. Discussion

1. Foraging Strategies

In both North Africa and Greece, *Cataglyphis bicolor* employs the same foraging strategy. It is a strictly individual forager. There is no kind of communication or group action, e.g. no kind of recruitment. Furthermore, *Cataglyphis* is specialized in scavenging. As the small items of dead animal matter exploited by the ants are distributed widely and unpredictably within the ants' habitat, individual foraging is a sensible strategy to deal with such a food distribution. Why this is so will be one point to be discussed subsequently.

Another point relates to the differences in certain foraging parameters as they occur between the Tunisian and Greek populations studied here. These differences can be traced back to differences in food density and availability. There is no a priori reason to assume that the differences in foraging behaviour between the North African and Greek ants are the result of intrinsic differences between the populations.

a) *Individual Foraging*: In Greece, *Cataglyphis bicolor* encounters much higher food densities than in Tunisia. This can be inferred even without direct measurements of food density from a number of foraging parameters. For example, the ants need less time to find a food item in Greece than they need in Tunisia (Tab. 2). Could such differences influence the foraging strategy? As has been shown experimentally by Hoelldobler and Wilson (1970) and Hoelldobler (1976), and later confirmed by the observations of Davidson (1977 a), North American harvester ants *Pogonomyrmex badius*, *P. rugosus*, and *P. barbatus* use group techniques when they forage in areas of high seed abundance, but may switch to individual techniques under less suitable conditions. No such change in the foraging strategy is found in *Cataglyphis bicolor* when the two populations are compared. At both sites the foragers invariably search individually. Oster and Wilson (1978) refer to this type of food searching behaviour as «diffuse» foraging. However, the behaviour of individual ants is by no means diffuse or random as this notation might suggest. Instead, individual foraging must be considered as an adaption to the type of food exploited. All the evidence at hand favours the hypothesis that the collected carcasses are widely dispersed and their presence is unpredictable in space and time. As further discussed by Schmid-Hempel (in prep.), such a type of food is best exploited by an individual foraging strategy.

At both study sites, foragers exhibit a high degree of individuality. This behaviour leads to the spatial partitioning of the foraging ground of the colony. Why, however, does each ant not leave the nest in another (random) direction every time it starts a new foraging run? For at least two reasons, this alternative sounds less reasonable. *First*, in any particular sector of the colony's foraging range food density may vary over periods of days, and this variation may be independent of the food density in other sectors.

Thus, at any one time, some sectors will be more profitable than others, so that it will pay the ant to return to a sector in which it has been successful before⁹. Let us recall, however, that within such a transient «macro-patch» (sector) food occurs unpredictably and widely spaced as far as the spatial dimensions of the ant's foraging activity are concerned. The *second* reason relates to the navigational strategies involved in foraging. Ants which repeatedly visit the same area have the possibility of acquiring some kind of landmark map, which can be used to back up the ant's vector navigation mechanism (Chapter IV.2).

b) *Niche Dynamics*. One of the most conspicuous differences between the Tunisian and Greek populations is a morphological one: The average size of the foragers is much smaller in Greece than it is in Tunisia. It seems that *Cataglyphis bicolor* can rather readily adapt its body size to local ecological conditions. The foragers are larger in more favourable areas (Delye, 1968) or at more favourable seasons (Schmid-Hempel, in prep.). Therefore, one should expect the foragers of the Greek population to be larger because it is at the Greek study site that food density is higher. However, just the opposite occurs. But why?

In Tunisia, a congeneric species, the smaller *Cataglyphis albicans*, occurs sympatrically. This species is suggested to be a major competitor of *Cataglyphis bicolor*. On the other hand, *Cataglyphis cursor*, the ecological equivalent of *Cataglyphis albicans* in southern Europe, does not occur at the site selected for this study in Greece (even though it occurs at other sites in Greece), nor is there any other species to take the place of *Cataglyphis albicans*. *Cataglyphis bicolor* is the sole scavenging forager at the time of day when it is active. There are others, for example *Pheidole pallidula*, but they are active mainly at other times of the day. The point we want to make in the following is that the difference in body size between the two populations of *Cataglyphis bicolor* might well be due to the presence or absence of a smaller congeneric competitor.

We can build up to the argument as follows: All species of *Cataglyphis* scavenge on dead arthropods. In general, the size distributions of arthropods present in any particular area, are skewed towards the smaller end of the scale (Janzen and Schoener, 1968). This has been confirmed for the Tunisian area by Schmid-Hempel (in prep.). Moreover, in Tunisia, the smaller *Cataglyphis albicans* exploits the smaller end of the size scale and thus has access to the more abundant food items. In Greece, where a smaller congeneric competitor is lacking, *Cataglyphis bicolor* obviously shifts its diet towards this more abundant end of the size scale. In turn, this leads to a reduction of the ants' sizes, since body size and food size are intimately related for metabolic reasons: It really does not pay for big-sized foragers to gather food items which are too small to compensate for the costs.

⁹ The crucial question how an individual ant selects *its* sector in the first place still remains to be answered.

There are a number of accounts which suggest that differences in body size allow otherwise similar species of ants to coexist. Such a correlation between body size and prey size has often been assumed. In many seed-harvesting ants, a correlation between preferred seed size and the sizes of foragers indeed exists (Hoelldobler, 1976; Oster and Wilson, 1978; Davidson, 1978; Hansen, 1978; Whitford, 1978a, b). One should be careful, however, about generalizing this statement too readily. First, the correlation between food and body size often does not apply in ant species which retrieve prey by co-operative social interactions (Hoelldobler et al., 1978; Oster and Wilson, 1978; Adams and Traniello, 1981). Secondly, changes in morphology need not affect the average body size alone. Davidson (1978) and Herbers (1980) point out that changes in the amount of variation of a particular trait within the colony might be more important than changes in the average value. For example, in *Veromessor pergandei* (Davidson, 1978) the variation in the body sizes of the workers increases when the number of co-existing competitors is reduced. The same conclusion can be drawn from our *Cataglyphis* data (Fig. 3). The coefficient of variation as calculated from our data on head width is 0.26 ($n = 90$) in Greece, but only 0.10 ($n = 304$) in Tunisia ($p < 0.001$). Taken together, different niche characteristics account for the morphological difference which exists between the foragers of both populations. This niche shift is reasonably well explained by some kind of ecological release (Van Valen, 1965; Oster and Wilson, 1978) induced by the absence of a smaller competitor in Greece.

As argued above, the smaller body sizes of the Greek foragers as compared to the Tunisian foragers allow for the exploitation of a more abundant food source. It is therefore not surprising that, in addition, the sizes of the foraging ranges are considerably smaller in Greece than they are in Tunisia. This is in accord with a number of reports that the size of the foraging range is decreased whenever the conditions become more favourable (Bernstein, 1975; Davidson, 1977 a; Bernstein and Gobbel, 1979)¹⁰. However, a small foraging range cannot be managed in the same way as a larger one. In Greece, for example, the foraging runs last for much shorter periods of time than in Tunisia, but many more runs are made by an individual ant per day. Most remarkably, the runs are completed in much shorter time intervals in Greece than in Tunisia even if they are unsuccessful. While searching, the ants might thus rely on some kind of time expectation when to stop. In such a case, these time limits should be set by the average food availability of the environment¹¹.

¹⁰ These studies relate the size of the foraging range to gross indicators of food availability, e.g. the amount of precipitation. However, behavioural changes, in particular the choice of diet, and morphological character displacement are other aspects that should be considered. In the latter case, it is a well-known fact that the size of the foraging range is positively correlated with the body size of the animal (for ants see Bernstein, 1971, p. 50 f).

¹¹ A similar kind of reasoning is used in deriving theoretically the optimal stopping rules for animals which exploit patches of food (e.g. Charnov, 1976).

c) *Colony Structure*. How often a particular point of the environment is sampled by an ant depends not only on the behaviour of individual ants, but also on the number of foragers per colony and on the density of the colonies. The differences observed between the colony structures of the Greek and Tunisian populations might well be related to such factors. In Tunisia, the colonies comprise a main nest and several subsidiary nests, whereas in Greece all individuals of a colony are confined almost always to a single nest. This implies that in Tunisia, foraging ranges are larger and foraging densities smaller than in Greece. The polydomous structure of the Tunisian colonies seems to result from a compromise between having to search a large area for scarce food and avoiding the concentration of the searching activities near the same nest by too many foragers. A similar correlation between polydomous colony structure and extended foraging range has been demonstrated by Hoelldobler and Lumsden (1980) for African weaver ants, *Oecophylla longinoda*. On the other hand, *Cataglyphis* colonies must pay for decentralizing their foraging ranges by adopting a polydomous colony structure. As the colonies are monogynous, many social activities of the individual nests must be co-ordinated. This need reflects itself in the frequent exchange of individuals (interior workers, larvae, and pupae) between nests of the same colony. Besides these differences, in both populations the spatial distributions of the colonies seem to be governed by the same ecological rules: The nearest nest of an alien colony lies at a distance which corresponds with the outer edge of the foraging range. This distance is given by the radius of a circular area to which the whole forager force of a colony devotes about 90% of its total search time (Fig. 28).

d) *Predation Risk*. While foraging, the ants are continuously exposed to the risk of being attacked by predators. In Greece, an individual ant performs more foraging runs per day, each lasting for a shorter period of time than in Tunisia. Nevertheless, during a whole day, each individual ant forages for an average time of almost 200min at both sites (Tab. 2). As the life expectancies of the foragers are also the same at both sites (6 days), Tunisian and Greek ants suffer from the same risk of predation¹². This coincidence might be accidental. On the other hand, predation risk seems to be a major factor shaping foraging strategy as well as life history dynamics of *Cataglyphis* (Schmid-Hempel, in prep.). This conclusion is supported by recent results of Rissing (1981), demonstrating that individually foraging ants are more vulnerable to predation than group foragers. In the case of *Cataglyphis bicolor*, spiders of the genus *Zodarium* and robber flies account for most of the losses¹³.

¹² In the colonies kept in our Zurich laboratories individual workers of *Cataglyphis bicolor* have survived for a number of years.

¹³ The actual hazards that threaten any worker which ventures outside the nest are different at the two sites. In Greece, predation by the spider *Zodarium frenatum* imposes a heavy mortality on foragers that «guard» the nest entrance. This kind of predation occurs exclusively at dawn and dusk (see also Harkness, 1976). In Tunisia, predation by spiders and robber flies during a foraging run is the chief cause of mortality. Other hazards, e.g. aggressive interactions between ants, are also present, but our calculations show that predation alone is almost sufficient to explain the observed loss of foragers.

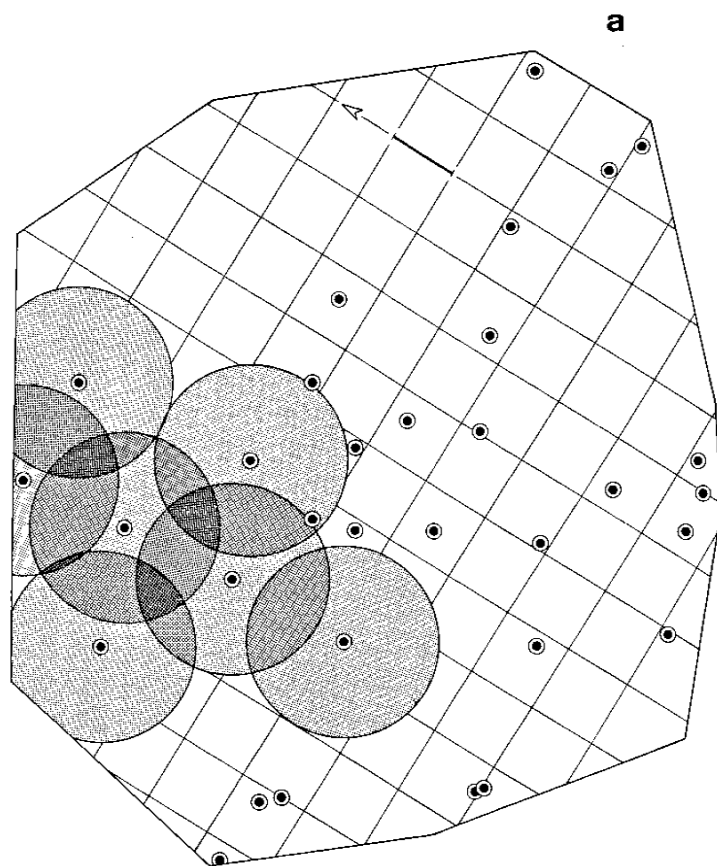
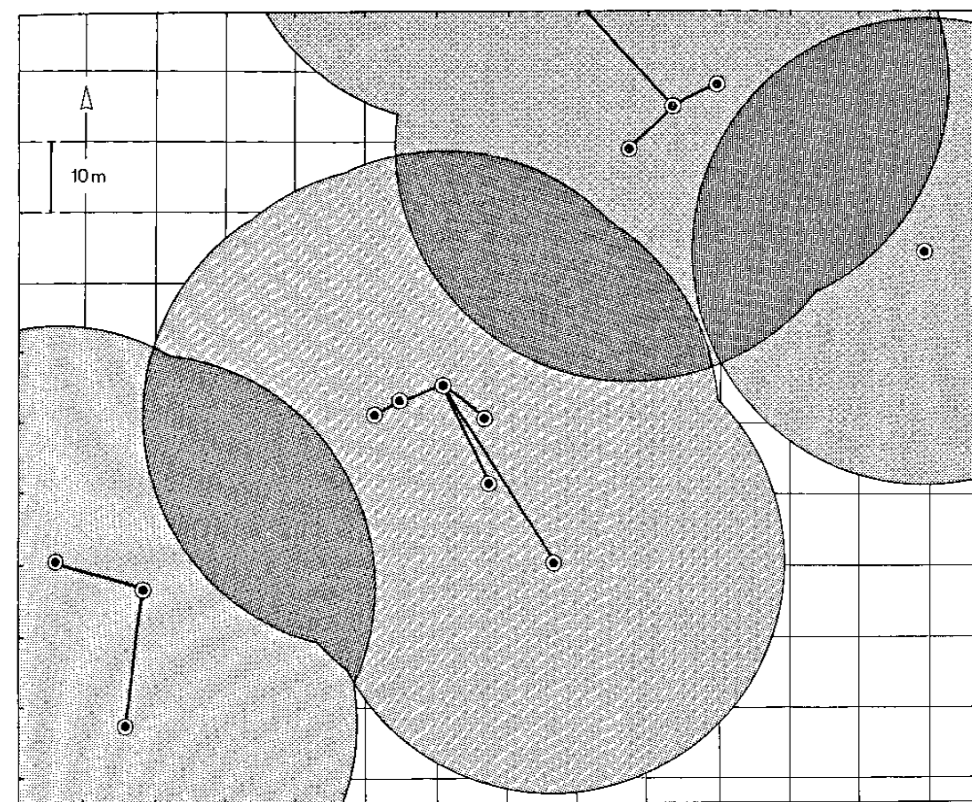


Fig. 1. Locations of nest sites (as in Fig. 1 a, b) and sizes of the foraging ranges (shaded areas) determined by colonies of *Cataglyphis bicolor* in Greece (a) and Tunisia (b). The foraging range is considered to be circular with a radius containing 90 % of the total search density (see Fig. 10).

The short life expectancies of *Cataglyphis* foragers imply that a colony must replace 20 % of its entire forager force every day. In other words, a colony which comprises 300 foragers must produce 30–60 workers a day to maintain its size. As shown by Schmid-Hempel (in prep.) such surprisingly high turnover rates do indeed occur.

Returns from Foraging. As dramatically shown by the former arguments, if a colony is to keep up its population, every forager must collect within its short lifetime at least a certain amount of food that is needed to grow up the larva which will replace it. How effective are individual foragers in this respect? At both study sites roughly 50 per cent of the foraging ants returned without food items to the colony. In Tunisia these ants had



failed to find anything. As compared to group foraging ants (Davidson, 1977b) the number is rather low and may reflect the price an individual forager must pay for adopting recruitment strategies. In Greece searchers were successful in over 90 % of their runs. Thus, nearly all the ants that returned carrying nothing in their jaws, about 50 %, were lickers.

To answer the question posed above – how efficient is an individual forager in replacing its biomass within the colony? – the total amount of food gathered by a forager during its entire lifetime (M) is a more crucial number. It can be calculated by multiplying the average weight of a food item (m) by the number of successful runs (n) during its lifetime. The latter quantity is derived from the average life-expectancy ($T = 6$ days) and the number of runs per day (n). As mentioned above, the proportion of runs (e) in which a food item is brought in is nearly the same at both sites, about half ($e = 0.5$). Calculated from $M = m \cdot T \cdot n \cdot e$, in Tunisia each forager delivers within its lifetime 467

fresh weight of food to its colony ($n = 4.2$, $m = 37.1$ mg; see Tab. 2). In Greece, the corresponding number is 165 mg ($n = 9.5$, $m = 5.8$ mg; Tab. 2). How do these quantities relate to the average body weight of a forager? In the end, it is this biomass that must be replaced¹⁴. The average body weight of a forager is 27.3 mg and 9.7 mg in Tunisia and Greece, respectively. Thus, during its entire lifetime a Tunisian *Cataglyphis bicolor* delivers 17.1 times its own body weight to the colony. In Greece, the corresponding number is 17.0. This comparison strongly suggests that the «foraging machinery» of *Cataglyphis*, though operating in different ways at the two study sites, yields the same returns.

2. Navigational Strategies

As it appears from the recording of individual foraging paths, an ant may repeatedly visit particular locations within its foraging range. It does not merely memorize the location where it has been successful last time, but other locations as well. To accomplish this task, it needs a map. In principle, *Cataglyphis* could rely on two types of map, a vector map or a landmark map. A *vector map* implies that the ants determine the directions and distances from the nest to particular points within their foraging range, and memorize all these pairs of polar co-ordinates (Fig. 29). This hypothesis could be tested most conveniently in an environment completely devoid of landmarks, so that there would be no way for an ant to determine positions by other means than using vector information. That *Cataglyphis* is able to perform vector navigation has been amply documented (Wehner, 1982a), but we have no data at hand to support the view that the ants store a number of compass bearings pointing at particular feeding sites¹⁵. Certainly, the ants use some kind of *landmark map* to specify locations of foraging sites. This is clearly borne out by experiments, not described in this paper, in which the ants change their individual foraging routes after the natural landmark panorama has been modified artificially. It can also be inferred from the common observation that the spatial layout of individual foraging paths is markedly affected by the distribution of landmarks within the ant's spatial environment. Further evidence derives from the

¹⁴ For this calculation, we neglect the material collected by lickers in Greece and the berries which are collected by the ants in Tunisia, arguing that this type of food is an energy source which drives the whole system, but is not needed as protein material to make new ants. In this case, the average fresh weight of a food item is 37.1 ± 4.5 mg ($n = 76$). A more exact analysis would require to take into account the dry weights or energetic contents of consumers and their food. However, by assuming these quantities to be relatively the same, we think it is justified to use the crude ratio of fresh weights.

¹⁵ To date, it is not known whether any animal species is able to establish and use a vector map. In recent summaries on animal navigation (Schoene, 1980; Merkel, 1980; Gauthreaux, 1980; Papi and Wallraff, 1982), the possibility of navigating by vector maps is not mentioned at all. Wallraff (1974) and Wiltshko and Wiltshko (1978) discuss how birds could pilot by «directionally oriented maps of familiar landmarks». In these «mosaic maps» the positions of landmarks are defined in terms of compass courses to be steered when moving from one landmark to another.

experiments on homing by artificial landmark cues (Section III. 6.c). Even in species of ants which engage in mass-foraging along scent trails, route fidelity depends, at least to a certain degree, on panoramas (*Pogonomyrmex* spp.: Hoelldobler, 1976; *Formica rufa*: Rosengren, 1971; Rosengren and Pamilo, 1978; Zakharov, 1978; *Camponotus modoc*: David and Wood, 1980). In a most interesting experimental study Hoelldobler (1980) has recently shown that African stink ants (*Paltothyreus tarsatus*, Ponerinae) use the pattern of the forest canopy for navigating back to the nest.

As deduced from our work on *Cataglyphis*, the ant's landmark map differs considerably from a map used by human navigators (Wehner, in press). Whereas a human navigator relies on a map in which the positions of landmarks are defined in absolute terms and not just relative to the paths actually taken, it is obviously the latter strategy that the insect applies. Correspondingly, the ant's «map» does not completely cover the area visited during consecutive foraging trips, but consists mainly in familiar «routes» passing through that area. According to this concept, each route is defined by a certain sequence of landmark images which the ant expects to appear in succession while proceeding along its foraging or homing paths. In these images, distances and sizes of landmarks are confounded. Thus, the piloting ant seems to use a sequential map based on relying on sequences of two-dimensional images of its landmark surroundings. Apparently, it is unable to develop the concept of a topographical map, in which landmarks are defined in three-dimensional space. Recently, Cartwright and Collett (1982) have proposed a quantitative model of how honeybees use landmarks to guide their return to a food source. The assumption underlying this model is completely in accord with what we have found in ants.

Provided with a sequential map, the insect should fail to compute the direct route from point A to point B when it has previously travelled to A and B only from a third point C. A close inspection of all the foraging paths which we have recorded at both experimental stations is in favour of this view¹⁶, but any final generalization must await direct experimental proof. Such experiments have high priority in our future work.

Using landmark information and using vector information are certainly not mutually exclusive strategies. While foraging, *Cataglyphis* always relies on vector navigation (dead reckoning), irrespective of the presence or absence of landmarks. But the more often an ant has travelled along a particular vector route, the more likely it will build up in its mind a sequential landmark map of that route. Hence, vector information might provide a reference system for establishing a landmark route. According to this hypothesis, landmarks are used to indicate a route which the ant would have taken anyway by relying on its dead reckoning system. Dead reckoning, however, is an intrinsically noisy system, and vector information provided by this system becomes the

¹⁶ The conclusion is also supported by studies of trap-lining behaviour in bumblebees (males: Haas, 1966; females: Heinrich, 1976) and orchid bees (Janzen, 1974). Particular sites are visited successively according to the temporal sequence in which they have become incorporated into the route.

only short-dated information about the ant's current position relative to home (when the ant is foraging) and about the position of the last finding site (when the ant is at home). Memory images of landmark routes might be more persistent. This would mean that the ant's map consisted of a number of landmark routes rather than a set of vectors. Consider, however, that even then the term «map» is used in a figurative rather than literal sense of the word.

V. Conclusion

In ants, indeed in any social insect, workers are just foraging machines. So powerful is the selection for efficient foraging strategies in these animals that it can be expected to have carried the evolution of appropriate systems of navigation along with it. From this point of view, the ultimate cause of the refined neural circuitry involved in a particular kind of navigation is nothing but the need to enhance foraging efficiency. In evolutionary terms, foraging strategies and navigational strategies are inextricably intertwined.

By appreciating this interrelationship we gain the proper framework for understanding the evolutionary design of the neural strategies which the insect has at its disposal. Apart from this framework, the insect's strategies used in navigation might appear inaccurate, ambiguous, and so much tailored to particular ecological needs within a particular environment that they cannot be generalized to apply to any other situation. Often, the impression seems inescapable that a perfect engineer, and a cyberneticist, would certainly have come up with something better.

In particular, in reading compass information from the sky, the ant – like the bee – relies on some simple rules of thumb. In terrestrial navigation, as considered in more detail in the present account, the ant does not establish and use a topographical map or floor plan of the arrangement of landmarks around its nest. It does not adopt a bird's eye point of view, but remains within the local world of its skyline pictures. Why is this so? Why have the ants arrived at local rather than more general, global solutions?

One way to answer such questions is to inquire about the adaptive significance of the navigational strategies involved in foraging. The main result of this inquiry is that the foraging activity of any particular *Cataglyphis* ant is extremely limited in both space and time. During its entire lifetime, an average individual ant makes not more than about 20–30 foraging trips spread over a period of 4–6 days. All these foraging trips are restricted to a small sector around the nest measuring 50–60° in width and 30–40m in radial length (Tunisian data).

Why is the foraging ground of the whole colony so strictly partitioned among individual ants? Obviously, the answer lies in the kind of foraging strategy which a scavenger on widely dispersed animal matter must adopt. For two reasons, natural selection does not allow the ants to potter around in a leisurely manner. First, the number of food items available per unit area and day is limited. Each day, the ants deplete their food sources, so that the density of food declines towards the afternoon. Second, the pressure exposed on *Cataglyphis* by predators is high and provides the truly limiting factor for the lifetime of the foraging ant. Therefore, a *Cataglyphis* forager must find food and return to the nest as quickly as possible. Otherwise, its contribution to the colony, and hence to the next generation, is likely to become zero. This demand calls for high walking speeds and efficient strategies of navigation. Indeed, *Cataglyphis* is one of the most rapidly walking ants. Furthermore, as an individually searching forager

must find its way by itself, it may profit by relying on familiar landmark routes, thus confining all foraging trips to a limited area.

In referring to landmark cues, *Cataglyphis* does not establish and read a map, but uses landmark information mainly to back up its dead reckoning system that is continuously operating anyway. Constructing a map needs time and elaborate triangulation, which *Cataglyphis* cannot afford. Left with a few foraging trips, it will encounter neither the possibility nor the need to acquire a topographical map of its landmark surroundings. In terms of foraging ecology, each of the categories mentioned above blends and intergrades with the next: food distribution, searching strategy, partitioning of the foraging grounds, walking speed, and strategies of navigation. With respect to the latter, there is at least one further constraint set by foraging ecology. For an ant that searches individually over an extended area, and must do so in as short a time as possible, the most efficient way to navigate is by visual means: by using the celestial cues as a compass and visual landmarks for piloting. Indeed, *Cataglyphis* is a visual navigator – and a truly diurnal insect.

Inquiring about the ant's navigational strategies in more detail, the human investigator might be surprised to find that the ant does not solve a particular problem the way he would. Given the ecological constraints as described in this paper, this is not astounding. However, it might humble the theorizing neurobiologist when he tries to interpret the bits of information he has at hand in terms of the «correct» way of conceiving of the problem.

V. Acknowledgements

Since the early seventies various aspects of visual orientation and foraging have been studied in *Cataglyphis bicolor* at both experimental sites, Platamon (R. H.) and Maharès (R. W.). Most recently (1980, 1981), P. S. focused specifically on the foraging ecology of the species while doing his Ph. D. work at Maharès. In August 1979, 1980, and 1981, R. H. and R. W. were able to join their efforts at Platamon. Much of the evaluation of the data was done at R. H.'s residence near London. R. W. joyfully remembers the kind hospitality he received at Rough Hey. We are all very grateful to our wives, Margaret Harkness, dipl. nat. Sibylle Wehner-von Segesser, and dipl. nat. Regula Schmid-Hempel. Without their help and co-operation in the field this work could not have been accomplished.

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VII. Summary

The foraging behaviour of the ant *Cataglyphis bicolor* is investigated at two study sites, Tunisia and Greece. In association with climatic differences (annual rainfall 400–200 mm in Tunisia, 800–1000 mm in Greece), food density is much higher at the Greek than at the Tunisian study site. Consequently, the population densities of *Cataglyphis bicolor* in Greece and Tunisia are different, 46'500 ants per ha and 7'000 ants per ha, respectively. The foraging strategies of the Greek and Tunisian populations are compared and discussed in terms of how they depend on food density.

The Greek populations have previously been assigned to a separate species, *Cataglyphis nodus*. New evidence is given that this taxonomical distinction cannot be maintained and that the populations occurring in North Africa and the Eastern Mediterranean area belong in fact to the same species, *Cataglyphis bicolor*.

Like all species of the genus, *Cataglyphis bicolor* is a scavenger searching for widely dispersed food items (mainly dead arthropods). It is a strictly diurnal forager leaving the nest individually and never undertaking mass foraging. Each individual ant restricts its foraging activity to a small part of the nest environment. As a consequence, the foraging ground of the colony is partitioned among the workers.

In Greece foragers are substantially smaller (head width 1.73 ± 0.05 mm) than in Tunisia (head width 2.62 ± 0.02 mm). This difference can be accounted for by the absence or presence of a smaller congeneric competitor at the Greek and Tunisian study sites, respectively. In Tunisia, the smaller *Cataglyphis albicans* occurs sympatrically. As size of food and body size of the foragers are correlated, the more abundant smaller food items are exploited by *Cataglyphis albicans* in Tunisia, but can also be exploited in addition to the larger items by *Cataglyphis bicolor* in Greece.

The foraging range of a colony can be approximated by a circular area centred around the nest. The radius of a circular area within which the ants spend 90 per cent of their foraging time, is 13 m in Greece and 32 m in Tunisia. This difference is due to the differences in food density, food size, and forager size occurring between both sites. The distances between nearest neighbour colonies correspond nicely with the sizes of the foraging ranges. Thus, the density of the colonies is much lower in Tunisia than in Greece.

The regional differences concerning the sizes of the foraging ranges are correlated with differences in foraging behaviour. In the mean, the foraging runs last only 19 min in Greece, but 53 min in Tunisia, irrespective of whether a food item has been found.

On the other hand, the ants make about 10 runs per day in Greece, but only 4 runs per day in Tunisia. At both sites, any particular ant leaves the nest repeatedly during the entire duration of the day, but in Greece the activity of the ants starts earlier in the morning and finishes later in the evening than in Tunisia. Nevertheless, a total foraging time of about 200 min per ant and day holds for both study sites.

7. In Tunisia, the colonies consist of one main nest housing the queen, and 2–5 subsidiary nests about 10 m apart from the main nest. This dispersed structure of the colony corresponds with the size of the foraging range which is considerably larger in Tunisia than in Greece. At the latter site, a colony is usually restricted to a single nest. In spite of this difference, similar numbers of workers per colony attend the foraging tasks at both sites (about 270 and 340 foragers per colony in Greece and Tunisia, respectively). At any one time, about 15 per cent of all colony members engage in foraging.

8. At both sites about half of the foragers return with solid prey (dead arthropods). The life expectancies of the foragers also coincide: 6 days per forager. Even though important foraging parameters (food size, forager size, number of foraging runs per day and ant) vary between the two sites, the overall intake of solid food is nearly the same. During its lifetime, each forager retrieves a food weight which is 15 to 20 times its average body weight.

9. At any one time and at any one place, a forager knows where it is relative to home. Furthermore, it is able to remember a number of foraging sites within its foraging range. The navigational abilities involved are intimately related to the problems imposed by adopting an individual foraging strategy. Navigation relies mainly on visual cues. The strategies employed are dead reckoning (vector navigation by means of celestial compass) and piloting by landmarks. At both study sites, any particular forager continuously performs vector navigation, but the extent to which vector navigation is backed up by piloting depends crucially on the availability of landmarks. At the Greek site landmark cues are much more abundant and pronounced in Greece than in Tunisia. The accuracy of navigation is improved at the former place.

10. Piloting strategies have been investigated by using sets of artificial landmarks. For pin-pointing the position of the nest, the ants establish and use two-dimensional memory images of the landmark surroundings as seen from the nest. When foraging, they rely on sequences of memory images, but do not adopt the concept of a true topographical map.

We wish to express our sincere gratitude to our Arab and Greek friends, whose helpful understanding was as necessary in accomplishing this work as it was delightful.

Zusammenfassung

Beutesuchstrategien bei solitär jagenden Wüstenameisen (*Cataglyphis bicolor*, Hymenoptera: Formicidae).

1. Die Navigationsleistungen von *Cataglyphis bicolor* werden im Rahmen einer verhaltensökologischen Analyse der Beutesuchstrategie der Art diskutiert. Anhand dieses Vorgehens lassen sich die ökologischen Anforderungen definieren, die jedes bei der Beutesuche eingesetzte Navigationssystem zu erfüllen hat und auf die hin es evolutiv angelegt worden ist. Da *Cataglyphis bicolor* einzeln jagt, wegen ihrer Größe, Auffälligkeit und der offenen Struktur ihres Jagdgeländes leicht individuell zu markieren und zu verfolgen ist und zudem während ihrer gesamten Lebensdauer nur eine begrenzte Zahl von 25–50 Beutesuchläufen absolviert, stellt sie für eine solche verhaltensbiologische Analyse ein geradezu ideales Versuchsobjekt dar.

Um die Invarianten des Beutesuchverhaltens herauszuarbeiten, werden zwei in ihren ökologischen Bedingungen recht unterschiedliche Standorte verglichen: Maharès (Tunesien) und Platamon (Griechenland). Gemäß den klimatischen Unterschieden zwischen beiden Gebieten (mittlerer jährlicher Niederschlag 100–200 mm in Maharès, 100–1000 mm in Platamon) weist das Versuchsgelände in Griechenland ein weit höheres Futterangebot als das in Tunesien auf. Dem entspricht die in Griechenland wesentlich höhere Populationsdichte von *Cataglyphis bicolor* (46'500 Individuen/ha gegenüber 7'000 Individuen/ha in Tunesien). Suchstrategien und beteiligte Navigationsmechanismen werden im Hinblick auf das unterschiedliche Futterangebot verglichen.

2. Taxonomisch hat man die griechischen Populationen gelegentlich einer eigenen Art (*Cataglyphis nodus*) zugeordnet. Neue Befunde zeigen eindeutig, daß diese taxonomische Unterscheidung nicht gerechtfertigt ist und die nordafrikanischen wie die osteuropäischen und vorderasiatischen Formen einer gemeinsamen Art (*Cataglyphis bicolor*) angehören.

3. Als Beuteobjekte dienen *Cataglyphis bicolor* wie allen Arten der Gattung vorwiegend kleine Arthropoden, die im Gelände räumlich weit und nahezu stochastisch verteilt sind, jedenfalls keine ausgeprägten «patches» bilden. Bei der Beutesuche, die nur tagsüber erfolgt, beschränkt jedes Individuum seine Suchaktivität während seiner gesamten Lebensdauer auf einen eng begrenzten Bereich der Nestumgebung. Auf diese Weise wird das Beuteareal einer Kolonie räumlich auf einzelne Individuen aufgeteilt. Rekrutierung oder andere Arten intraspezifischer Kooperation fehlen bei der Beutesuche.

4. Die Körpergröße liegt bei der tunesischen Population signifikant höher als bei der griechischen (Kopfbreite der Außendiensttiere 2.62 ± 0.02 mm in Maharès und $1.73 \pm$

0.05 mm in Platamon). Dieser Unterschied läßt sich auf das sympatrische Auftreten einer kleineren, konkurrierenden *Cataglyphis*-Art (*Cataglyphis albicans*) in Tunesien zurückführen. Im griechischen Versuchsgelände fehlt dieser oder ein äquivalenter Konkurrent. Da Größe der Beuteobjekte und Körpergröße der Außendiensttiere korrelieren, kommt es in Tunesien zu einer größenmäßigen Aufteilung des Futterspektrums zwischen beiden Arten. In Griechenland steht *Cataglyphis bicolor* dagegen das gesamte Beutespektrum zur Verfügung. Folglich zeigt auch die Größenverteilung der griechischen *Cataglyphis bicolor* einen breiteren und zu niedrigeren Werten verschobenen Verlauf.

5. Das Beutesuchareal einer Kolonie kann durch eine kreisförmig um das Nest zentrierte Fläche angenähert werden. Der Radius eines solchen Kreises, in dem alle Individuen 90 % ihrer gesamten Suchzeit verbringen, beträgt 13 m in Griechenland und 32 m in Tunesien. Diese markante Differenz läßt sich auf die geschilderten regionalen Unterschiede bezüglich Beutedichte, Beutegröße und Körpergröße der Außendiensttiere zurückführen. Die Entfernungen zwischen den Standorten benachbarter Kolonien entsprechen den Radien der 95 %-Futtersuchareale. Die Koloniedichte liegt daher in Tunesien weit unter derjenigen in Griechenland.

6. Die regionalen Größenunterschiede zwischen den Beutesucharealen sind mit entsprechenden Unterschieden im Beutesuchverhalten der Einzeltiere korreliert. Unabhängig davon, ob ein Beuteobjekt gefunden wird oder nicht, dauern die Beutesuchläufe in Griechenland im Mittel 19 min, in Tunesien 53 min. Andererseits führt eine griechische *Cataglyphis bicolor* im Mittel 10, eine tunesische nur 4 Beutesuchläufe/Tag aus. Die 10 Beutesuchläufe werden in Griechenland auf eine größere Zeitspanne des Tages verteilt als die 4 Beutesuchläufe in Tunesien. Die mittlere tägliche Beutesuchzeit eines Individuums stimmt jedoch an beiden Versuchsplätzen überein. Sie beträgt ca. 200 min/Individuum/Tag.

7. In Tunesien bestehen die Kolonien aus einem Hauptnest, das die Königin enthält, und 2–5 Nebennestern in ca. 10 m Abstand voneinander. Diese aufgelöste Koloniestruktur entspricht der beträchtlichen Größe des in Tunesien von einer Kolonie abgedeckten Beutesuchareals. In Griechenland mit seinen wesentlich kleineren Beutesucharealen ist eine Kolonie in der Regel auf ein Nest beschränkt. Trotz dieses Unterschiedes stimmt die Zahl der im Außendienst tätigen Individuen einer Kolonie an beiden Versuchsplätzen überein (im Mittel 270 Außendiensttiere/Kolonie in Griechenland und 340 Außendiensttiere/Kolonie in Tunesien). Da die Außendiensttiere in beiden Fällen ca. 15 % der gesamten Individuenzahl einer Kolonie ausmachen, weisen die Kolonien der nordafrikanischen und südosteuropäischen Populationen gleiche Stärken auf.

8. An beiden Versuchsplätzen beträgt die Beutesucheffizienz 50 %: Jeder zweite Beutesuchlauf bringt der Kolonie ein Beuteobjekt ein. Unter den restlichen 50 % befindet sich ein großer Prozentsatz von Tieren, die kohlenhydratreiche Nahrung (Pflanzensekrete) eintragen. Auch die mittlere Lebenserwartung während des Außendienst-Stadiums stimmt in Griechenland und Tunesien überein. Sie beträgt 6 Tage/Individuum. Der hohe Räuberdruck (vor allem durch Spinnen und Raubfliegen) zeichnet für diese geringe Lebenserwartung verantwortlich. Berechnet man anhand dieser beiden Größen sowie der an beiden Versuchsplätzen unterschiedlichen Werte für Beutegröße, Körpergröße der Außendiensttiere und Anzahl Beutesuchläufe pro Tag den gesamten Futtereintrag pro Individuum, erhält man ein überraschend einheitliches Ergebnis: In Griechenland und Tunesien trägt jede *Cataglyphis bicolor* im Laufe ihres Lebens das 15- bis 20fache ihres eigenen Körpergewichts ein.

9. Die bei der Beutesuche eingesetzten Navigationssysteme sind eng mit der Art der individuellen Suchstrategie korreliert. Sie bedienen sich fast ausschließlich visueller Orientierungsreize. Über einen Vektor-Navigations-Mechanismus (mit Hilfe eines astronomischen Kompasses) ist jedes Individuum zu jedem Zeitpunkt über seine relative Position zum Ausgangspunkt (Nest) orientiert. Zusätzlich werden die eingeschlagenen Routen über ein Pilotierungs-System anhand terrestrischer Panorambilder markiert. Das Ausmaß, in dem das ständig laufende, aber relativ unpräzise Vektor-Navigations-System vom Pilotierungs-System unterstützt wird, hängt von der Struktur der verfügbaren terrestrischen Marken ab. Da solche Marken im griechischen Versuchsgelände weit häufiger und ausgeprägter sind, steigt hier die Navigationsgenauigkeit.

10. Der Mechanismus des Pilotierens wird experimentell mit Hilfe künstlicher Landmarkenkonfigurationen untersucht. Bei der Beutesuche bedient sich *Cataglyphis bicolor* nicht des Konzepts einer dreidimensionalen topographischen Landmarkenkarte, sondern Sequenzen von «eidetischen» Erinnerungsbildern, die das Nest mit einzelnen Geländepunkten verbinden. Diese Art des Pilotierens, die sich eines Vergleichs von memorierten und aktuellen Retina-Bildern bedient, arbeitet mit den scheinbaren, nicht den wahren (absoluten) Größen der terrestrischen Objekte. Sie funktioniert daher nur, wenn sich die Ameise auf einer gegebenen Route befindet und ihr die Landmarken von den einzelnen Punkten der Route stets unter gleichem Blickwinkel erscheinen. Da sich *Cataglyphis bicolor* während ihrer gesamten Lebensdauer stets des gleichen Beutesuchareals bedient, ist diese Bedingung erfüllt. Absolute Geländekenntnis, d. h. der Besitz einer topographischen Karte, die unabhängiges Navigieren zwischen beliebigen Geländepunkten erlaubt, ist nicht erforderlich.

Unseren arabischen und griechischen Freunden, ohne deren verständnisvolle Hilfe diese Arbeit nicht möglich gewesen wäre, danken wir herzlich.

Résumé

Stratégie de fourragement de la fourmi cherchant individuellement, *Cataglyphis bicolor* (Hymenoptera: Formicidae).

1. Le comportement de fourragement de la fourmi *Cataglyphis bicolor* a été étudié en Tunisie et en Grèce.

En raison des différences de climat (de 100 à 200 mm de pluie en Tunisie et de 800 à 1000 mm en Grèce) la quantité d'alimentation disponible est beaucoup plus considérable en Grèce qu'en Tunisie. Par conséquent, la densité de la population *Cataglyphis bicolor* en Grèce est de 46'500 fourmis par ha et en Tunisie de 7'000 fourmis par ha. Les stratégies de fourragement des populations en Grèce et en Tunisie sont discutées en comparant leur dépendance de la quantité alimentaire.

2. Les populations grecques ont jusqu'à présent été classées comme appartenant à une autre espèce, *Cataglyphis nodus*. Nous avons aujourd'hui la preuve que cette distinction taxonomique ne peut pas être retenue et que les populations existant en Afrique du Nord et dans la région à l'est de la Méditerranée appartiennent à la même espèce, *Cataglyphis bicolor*.

3. Comme toutes les espèces appartenant au même genre, *Cataglyphis bicolor* est un nécrophage cherchant des pièces d'alimentation très dispersées (essentiellement des arthropodes mortes). Il s'agit d'une fourrageuse exclusivement diurne quittant sa fourmilière individuellement sans jamais fourrager en groupe. Chaque fourmi limite son activité de fourragement à un petit territoire à proximité de la fourmilière. Par conséquent, le domaine de fourragement de la colonie est morcelé par les ouvrières.

4. En Grèce, les fourrageuses sont beaucoup plus petites (largeur de la tête 1.73 ± 0.05 mm) qu'en Tunisie (largeur de la tête 2.62 ± 0.02 mm). Cette différence s'explique par l'absence ou la présence d'un concurrent congénérique plus petit. En Tunisie, *Cataglyphis albicans*, qui est plus petite, existe dans la même région. Puisqu'il y a une corrélation entre volume des pièces alimentaires et grandeur de la fourrageuse, les petites pièces d'alimentation qui sont abondantes sont consommées par *Cataglyphis albicans* en Tunisie. En Grèce, *Cataglyphis bicolor* consomme des pièces plus larges sans pour autant mépriser les pièces plus petites.

5. Le domaine de fourragement d'une colonie peut se situer dans un rayon circulaire autour de la fourmilière. Le rayon circulaire dans lequel des fourmis passent 90 pour cent de leur temps de fourragement mesure 13 m en Grèce et 32 m en Tunisie. Cette différence s'explique par la densité et le volume des pièces alimentaires et la taille de la fourrageuse. Les distances entre les colonies avoisinantes correspondent à l'étendue du

domaine de fourragement. Par conséquent, la densité des colonies est bien moindre en Tunisie qu'en Grèce.

5. Il y a une corrélation entre les différences régionales des dimensions des domaines de fourragement et les différences dans le comportement de fourragement. En moyenne, les excursions de fourragement ne durent que 19 minutes en Grèce, mais 53 minutes en Tunisie, sans tenir compte si une pièce d'alimentation a été trouvée ou non. Les fourmis de Grèce font approximativement 10 excursions par jour, en Tunisie, par contre, seulement 4. Aux deux endroits, toute fourmi quitte la fourmilière à plusieurs reprises du matin au soir, mais en Grèce, les fourmis commencent leur activité plus tôt le matin et la terminent plus tard le soir que les fourmis de Tunisie. Néanmoins, le temps total de fourragement est d'environ 200 minutes par fourmi et par jour en Tunisie comme en Grèce.

En Tunisie, la colonie consiste en une fourmilière principale où se trouve la reine, et 2 à 5 fourmilières secondaires à 10 m de distance environ de la fourmilière principale. Cette structure dispersée de la colonie correspond au domaine de fourragement considérablement plus vaste en Tunisie qu'en Grèce. En Grèce, une colonie ne comporte généralement qu'une fourmilière. Malgré cette différence le nombre d'ouvrières par colonie qui accomplissent les tâches de fourragement ne diffère que de peu (env. 70 en Grèce et 340 en Tunisie). Environ 15 pour cent des membres d'une colonie sont constamment occupés à des tâches de fourragement. Cela, c'est le cas en Grèce comme en Tunisie.

En Grèce comme en Tunisie, l'efficacité de fourragement est d'environ 50 pour cent. Lors d'une excursion sur deux la fourmi rapporte une pièce d'alimentation. Il y a aussi une coïncidence en ce qui concerne la durée de la vie: 6 jours par fourmi. Et malgré le fait que les paramètres de fourragement (volume d'alimentation, grandeur de la fourrageuse, nombre d'excursions par jour et par fourmi) divergent largement, la consommation de nourriture est quasiment la même chez les fourmis de Grèce et de Tunisie. Pendant la durée de sa vie, chaque fourrageuse apporte des aliments d'un poids 15 à 20 fois supérieur au poids de son corps.

Toujours et partout, une fourrageuse sait s'orienter par rapport à sa fourmilière. Elle est aussi capable de se rappeler d'un nombre de sites de fourragement à l'intérieur du domaine de fourragement. Ses capacités de navigation sont en corrélation avec les problèmes créés par l'adoption d'une stratégie de fourragement individuelle. La navigation se base essentiellement sur des indications visuelles. Les stratégies sont: navigation par vecteur à l'aide d'une boussole astronomique et pilotage par repères terrestres. En Grèce comme en Tunisie, toutes fourrageuses naviguent continuellement par vecteur, mais dans une proportion dans laquelle la navigation par vecteur est renforcée par le pilotage

dépend fortement du nombre de repères terrestres disponibles. Les repères terrestres sont beaucoup plus nombreux et marqués en Grèce qu'en Tunisie, ce qui élève la précision de navigation en Grèce.

10. Des stratégies de pilotage ont été étudiées à l'aide d'une série de repères terrestres artificiels. Afin de situer la position de la fourmilière, les fourmis utilisent des images mémorisées à deux dimensions du repère terrestre vu de la fourmilière. En fourrageant elles se fient aux séquences d'images mémorisées sans toutefois adopter la conception d'une véritable carte topographique.

Nous voudrions exprimer notre gratitude envers nos amis arabes et grecs. Sans leur aide et sans leur compréhension, ce travail n'aurait pas pu être effectué.

ملخص

الأساليب التي تتبعها النملة من فصيلة كاتاجليفييس بيكولور (النملة الملونة) *Cataglyphis bicolor*, (Hymenoptera Formicidae) للبحث عن غذائها.

1- شملت الدراسة سلوك النملة من الفصيلة المذكورة أعلاه وأساليبها في البحث عن غذائها في كل من تونس واليونان.

ونظراً لاختلاف المناخ في البلدين (إذ يبلغ معدل الأمطار 100 إلى 200 مم في تونس و800 إلى 1000 مم في اليونان) فإن كميات غذاء النمل المتوفرة في اليونان تزيد عن تلك المتوفرة في تونس. وبالتالي، تبلغ كثافة النمل في اليونان 46500 نملة في هكتار، وفي تونس 7000 نملة في كل هكتار. لذلك، فإن دراسة أساليب مجموعات النمل في البحث عن غذائها في كل من تونس واليونان تستند إلى مقارنة اعتماد كل مجموعة على كمية الغذاء المتاحة.

2- كانت مجموعات النمل الموجودة في اليونان تدرج حتى الآن تحت فصيلة كاتاجليفييس نوديس (النملة السوداء) (*Cataglyphis nodus*) أما اليوم، فلدينا الدليل على أن هذا التمييز في التصنيف لا يُعتد به، وأن مجموعات النمل في شمال أفريقيا وفي منطقة شرق البحر الأبيض المتوسط تنتمي كلها إلى نفس الفصيلة أي فصيلة النملة الملونة.

3- تعتمد النملة الملونة، مثلها في ذلك مثل جميع الأنواع الأخرى من هذه الفصيلة، على الجيف بمختلف أنواعها (وهي تتغذى أساساً على الحشرات الميتة). وهذه النملة تخرج للبحث عن الغذاء أثناء النهار فقط. وهي تغادر الخلية وتمضي وحدها، ولا تخرج أبداً في مجموعات للبحث عن الغذاء. وتضع كل نملة لنفسها حدوداً في المنطقة الصغيرة التي تبحث فيها قرب الخلية. لهذا، نلاحظ أن منطقة البحث عن الغذاء تكون مقسمة حسب عدد النمل العامل.

4- إن حجم هذه النملة في اليونان أصغر من حجم مثيلتها في تونس (حجم الرأس بالنسبة لنملة اليونان: $0.02 + 0.05$ مم، وحجمه في تونس: $0.27 + 2.62$ مم). ويعود السبب في هذا الفرق إلى وجود نمل آخر من نفس الفصيلة وفي نفس المنطقة.

حجمه أصغر من النملة الملونة. وعلى سبيل المثال، توجد في تونس، في نفس المنطقة التي أجريت فيها الدراسة، نملة من فصيلة كاتاجليفييس البيكان (النملة البيضاء) (*Cataglyphis albicans*) أصغر حجماً من النملة موضوع الدراسة. ولما كانت هناك صلة بين كمية الغذاء وحجم النملة المنقبة عنه، فإن النملة البيضاء في تونس، وهي أصغر حجماً كما ذكرنا، تستهلك القطع الأصغر حجماً من الغذاء المتوفر. أما في اليونان، فإن النملة الملونة تستهلك القطع الأكبر حجماً (ولكنها، مع ذلك، لا تترك القطع الصغيرة).

5- تأخذ منطقة البحث عن الغذاء شكل دائرة حول الخلية. وتقضي النملة 90% من وقتها في البحث عن الغذاء داخل حدود هذه الدائرة التي يبلغ نصف قطرها 13 متراً في اليونان و32 متراً في تونس. وهذا الاختلاف في اتساع الدائرة يعود إلى اختلاف كثافة الغذاء المتوفر واختلاف أحجام العمل والمساحات الواقعة بين كل خلية وأخرى هي المساحات التي تغطيها مناطق البحث عن الغذاء لهذا السبب، نلاحظ أن عدد مستعمرات النمل في تونس يقل عن عدد مثيلاتها في اليونان.

6- هناك صلة بين مساحة المنطقة التي تبحث فيها النملة عن الغذاء والأسلوب الذي تتبعه في كل من البلدين. ففي المتوسط، تستغرق رحلة البحث عن الغذاء 19 دقيقة في اليونان و53 دقيقة في تونس، بغض النظر عن النتيجة التي تصل إليها النملة (أي حصولها أو عدم حصولها على قطعة من الغذاء). وتقوم النملة في اليونان بعشر رحلات في اليوم، أما النملة في تونس فتقوم بأربع رحلات فقط يومياً. وفي البلدين تخرج النملة من الخلية عدة مرات في اليوم. إلا أن النملة في اليونان تبدأ رحلاتها مبكراً وتنتهيها في وقت متأخر من النهار، بعكس مثيلتها في تونس. ومع ذلك، يبلغ مجموع الوقت الذي تنفقه كل نملة في البحث عن الغذاء 200 دقيقة يومياً في تونس واليونان على السواء.

7- وتتكون مستعمرة النمل في تونس من خلية رئيسية حيث توجد الملكة، وخليتين إلى خمس خلايا ثانوية تبعد حوالي عشرة أمتار عن الخلية الرئيسية. وهذا التناثر في مواقع الخلايا يتناسب مع منطقة البحث عن الغذاء التي تكون أوسع في تونس عنها في اليونان. وفي البلد الأخير تشمل المستعمرة عادة خلية نمل واحدة. ورغم هذا الاختلاف، فإن عدد النمل العامل الذي يقوم بوظيفة البحث عن الغذاء لا يختلف كثيراً بين البلدين (فهو يبلغ 270 نملة في اليونان و340 نملة في تونس).

وتعمل نسبة قدرها 15% من النمل الموجود في كل مستعمرة في البحث عن الغذاء بصورة مستمرة. وينطبق هذا الوصف على مستعمرات النمل في تونس واليونان على السواء.

8- وفي اليونان، كما في تونس، يبلغ ناتج البحث 50% تقريباً، أي أن النملة تعود بقطعة غذاء في كل رحلة من رحلتين. وهناك تشابه بين عمر النملة في البلدين، إذ يبلغ ستة أيام للنملة. وعلى الرغم من الاختلاف الكبير بين البيانات المتعلقة بالبحث عن الغذاء (أي كمية الغذاء المتوفر، حجم النملة، عدد الرحلات التي تقوم بها كل نملة يومياً) فإن استهلاك الغذاء واحد لدى مجموعات النمل في البلدين. وتجمع كل نملة، خلال مدة حياتها، كمية من الغذاء تفوق وزنها 15 أو 20 مرة.

9- وتستطيع النملة الباحثة عن الغذاء أن تحدد، في أي وقت وأي مكان، موقعها بالنسبة للخلية. ويمكنها أن تتذكر عدة معالم أرضية معينة داخل منطقة البحث عن الغذاء. وهناك صلة مباشرة بين قدرتها على تحديد مسارها والمشكلات التي تواجهها أثناء بحثها عن الغذاء وأسلوبها الخاص في مواجهة هذه المشكلات. وتحدد النملة مسارها استناداً إلى مؤشرات بصرية. والأساليب المتبعة هي عادة نوع من «الملاحاة الفلكية» بمساعدة البوصلة والاستعانة بالمعالم الأرضية البارزة. وفي تونس، كما في اليونان، تستخدم النملة دائماً هذا الأسلوب «الفلكي» في تحديد مسارها. وتتوقف دقة هذا المسار إلى حد كبير على عدد المعالم الأرضية المتاحة. وفي اليونان يتجاوز عدد هذه المعالم البارزة عدد مثيلاتها في تونس، وهذا هو السبب في أن النمل في اليونان يحدد مساره بصورة أكثر دقة من النمل في تونس.

10- ولدراسة الأساليب المتبعة في تحديد المسار، تمت الاستعانة بمعالم بارزة موضوعة خصيصاً لهذا الغرض. وأتضح أن النمل، عندما يريد تحديد موقعه بالنسبة للخلية، يستخدم صوراً ذات بعدين، مخزّنه في الذاكرة، عن شكل المعلم الأرضي كما يبدو عند النظر إليه من الخلية. وتعتمد النملة، وهي سائرة، على تتابع هذه الصور المخزنة، وذلك دون الاعتماد على خريطة طبوغرافية حقيقية.

يسرنا أن نعرب عن خالص أمتناننا لأصدقائنا العرب واليونانيين الذين اتاحوا لنا، بفضل تعاونهم وتفهمهم، فرصة إعداد هذا البحث.

Περίληψη

Ἡ στρατηγική τῆς ἀναζήτησης τροφῆς στά μυρμηγκία τῆς ἐρήμου (*Cataglyphis bicolor*, ὑμενόπτερα: Formicidae), τὰ ὁποῖα κυνηγᾶνε τὴν λεία τους μεμονωμένα.

1. Ἐρευνήσαμε στὴν Ἑλλάδα στὸν Πλαταμῶνα καὶ στὴν Τυνησία στὸ Μαχάρες, κατὰ ποιὸ τρόπο τὰ μυρμηγκία *Cataglyphis bicolor* ψάχνουν τὴν τροφή τους. Ἀνάμεσα στοὺς δύο τόπους ὑπάρχουν μεγάλες κλιματικές διαφορές. Ἡ μεσαία ἐτήσια βροχόπτωση ἀνέρχεται στὰ 100–200 mm στὸ Μαχάρες καὶ 800–1000 mm στὸν Πλαταμῶνα.

Κατόπιν αὐτοῦ ὑπάρχει στὸ ἐλληνικὸ πειραματικὸ πεδίο παρὰ πολὺ περισσότερη τροφή ἀπ' ὅτι στὸ τυνησιακὸ. Αὐτὸ ἔχει σάν συνέπεια ὅτι στὴν Ἑλλάδα 46.500 μυρμηγκία *Cataglyphis bicolor* ζοῦν, ἐνῶ στὴν Τυνησία μόνο 7000.

2. Μερικοὶ ἐρευνητὲς μυρμηγκιῶν ταξινομήσαν τὰ νοτιοανατολικο-εὐρωπαϊκὰ μυρμηγκία σέ ἓνα ξεχωριστὸ εἶδος (*Cataglyphis nodus*). Νέα ἀποτελέσματα δείχνουν ὅμως ὅτι τὰ ἐλληνικά καὶ τὰ τυνησιακὰ μυρμηγκία ἀνήκουν στὸ ἴδιο εἶδος (*Cataglyphis bicolor*).

3. Ἡ τροφή τῶν *Cataglyphis bicolor* ἀποτελεῖται κυρίως ἀπὸ νεκρά ἔντομα καὶ ἄλλα ἀρθρόποδα. Αὐτὰ τὰ μέρη τροφῆς βρίσκονται διασκορπισμένα στὸ πεδίο. Κάθε μυρμηγκί ψάχνει σέ ἓνα στενὰ περιορισμένο τμήμα τῆς περιοχῆς γύρω ἀπὸ τὴν φωλιά. Κατ' αὐτὸ τὸν τρόπο διαχωρίζεται τοπικά ἡ περιοχὴ γύρω ἀπὸ τὴν φωλιά στὰ μεμονωμένα ἄτομα τῆς ἀποικίας. Τὰ μυρμηγκία δὲν δείχνονται συνεργάσιμα κατὰ τὴν διάρκεια τῆς ἀναζήτησης τῆς τροφῆς τους.

4. Στὴν Τυνησία τὰ *Cataglyphis bicolor* εἶναι πολὺ (οὐσιωδῶς) μεγαλύτερα ἀπὸ τὴν Ἑλλάδα. Στὸ Μαχάρες τὸ πλάτος τοῦ κεφαλοῦ τοῦ καθενὸς ἀνέρχεται στὸ μέσον 2,6 mm καὶ στὸν Πλαταμῶνα 1,7 mm. Ἡ αἰτία αὐτῆς τῆς διαφορᾶς ἐξηγεῖται στὸ ὅτι στὴν Τυνησία ἐμφανίζεται ἓνα μικρότερο εἶδος *Cataglyphis* τὸ (*Cataglyphis albicans*) σάν ἀνταγωνιστῆς. Τὸ μέγεθος τῶν κομματιῶν τῆς τροφῆς τὰ ὁποῖα μπορεῖ νὰ μεταφέρει ἓνα μυρμηγκί ἐξαρτᾶται φυσικά ἀπὸ τὸ μέγεθος τοῦ σώματος του.

Στὴν Τυνησία μάλιστα τὰ δύο ἀνταγωνιστικά εἶδη *Cataglyphis* πρέπει νὰ χωρίσουν τὴν προσφορά τροφῆς: Τὸ *Cataglyphis bicolor* μαζεὺει τὰ μεγάλα κομμάτια τροφῆς, τὸ *Cataglyphis albicans* μαζεὺει τὰ μικρά. Στὸ ἐλληνικὸ πειραματικὸ πεδίο τὸ *Cataglyphis bicolor* ἔχει ἀντιθέτως ὁλόκληρη τὴν προσφορά τροφῆς στὴ διάθεση του. Συνέπεια τούτου εἶναι ὅτι τὸ μέγεθος τοῦ σώματος τῶν ἐλληνικῶν *Cataglyphis bicolor* θὰ εἶναι μικρότερο.

5. Ἡ ἐπιφάνεια πάνω στὴν ὁποία ὅλα τὰ μυρμηγκία μᾶς ἀποικίας ψάχνουν τὴν τροφή τους, εἶναι στὴν Τυνησία σαφῶς μεγαλύτερη ἀπ' ὅτι στὴν Ἑλλάδα. Ἡ

διάμετρος ενός κύκλου, στον οποίο όλα τα άτομα περνούν περίπου το 90% του χρόνου τους είναι στην Ελλάδα 26 μέτρα και στην Τυνησία 64 μέτρα. Αυτή η διαφορά έγκειται στο ό, τι η τροφή είναι στην Ελλάδα πολύ περισσότερη από ό, τι στην Τυνησία.

Στην Τυνησία ένα *Cataglyphis bicolor* για να βρῇ ένα κομμάτι τροφή πρέπει να πάει πολύ πιο μακριά απ'ότι στην Ελλάδα. Αυτό έχει σαν αποτέλεσμα ότι και οι φωλιές στην Τυνησία βρίσκονται σε μεγαλύτερη απόσταση απ'ότι στην Ελλάδα. Η απόσταση ανάμεσα στις φωλιές αντιστοιχεί στο μέγεθος της επιφάνειας πάνω στην οποία ψάχνουν τα μυρμήγκια μιᾶς αποικίας για τροφή.

6. Η διαφορετική προσφορά τροφής στην Ελλάδα, και στην Τυνησία προϋποθέτει ότι τα μυρμήγκια στους δύο τόπους ψάχνουν κατά διαφορετικούς τρόπους για την τροφή τους. Ανεξάρτητα αν βρεθῇ τροφή ἢ ὄχι ἓνας γύρος διαρκεί στην Ελλάδα, 19 λεπτά και στην Τυνησία 53 λεπτά. Ένα ελληνικό *Cataglyphis bicolor* επιχειρεῖ κάθε μέρα 10 γύρους, ἓνα τυνησιακό αντιθέτως μόνο τέσσερις γύρους. Εάν υπολογίσουμε κανείς πόσο χρονικό διάστημα χρειάζεται ἓνα μυρμήγκι κάθε μέρα για ἀναζήτηση τροφής, τότε βρίσκει ότι και στά δύο πειραματικά πεδία αντιστοιχεί ἡ ἴδια τιμὴ δηλαδή 200 λεπτά ἀνά ἔντομο τὴν ἡμέρα.

7. Στην Τυνησία αποτελοῦνται οἱ ἀποικίες ἀπὸ μία κεντρικὴ φωλιά, στὴν ὁποία εἶναι ἡ βασίλισσα, καὶ 2-5 δευτερεύουσες φωλιές σε ἀπόσταση δέκα μέτρα περίπου ἢ μία ἀπὸ τὴν ἄλλη. Στην Ελλάδα ἡ ἀποικία περιορίζεται τὶς περισσότερες φορές σε μία μοναδική φωλιά.

Παρ' ὅλην αὐτὴν τὴν διαφορά, συμφωνεῖ ὁ ἀριθμὸς τῶν κυνηγῶν μέσα στὴν ἀποικία καὶ στά δύο πειραματικά πεδία (270 κυνηγοὶ ἀνά ἀποικία στὴν Ελλάδα καὶ 340 κυνηγοὶ στὴν Τυνησία). Τὸ ποσοστὸ τῶν κυνηγῶν ἀνέρχεται καὶ στίς δύο περιπτώσεις περίπου στὸ 15% ὅλων τῶν μυρμηγκιῶν μιᾶς ἀποικίας. Κατ' αὐτὸ ἐπιδεικνύουν καὶ οἱ δύο ἀποικίες στὴν Ελλάδα καὶ στὴν Τυνησία περίπου ἴδια δύναμη.

8. Καὶ στά δύο πειραματικά πεδία ἔχουν τὰ μυρμήγκια τὴν ἴδια ἐπιτυχία. Κάθε δεύτερο ψάξιμο φέρνουν ἓνα κομμάτι τροφῆς στὴν ἀποικία. Μέσα στὸ ὑπόλοιπο 90% ὑπάρχουν πολλὰ, τὰ ὁποία ἀπορροφοῦν φυτικούς χυμούς καὶ μεταφέρουν αὐτὴν τὴν ὑγρὴν τροφήν στὴν φωλιά. Ἡ διάρκεια ζωῆς συμφωνεῖ ἐπίσης στὴν Ελλάδα καὶ στὴν Τυνησία. Κάθε μυρμήγκι κυνηγὸς ζεῖ περίπου 6 ἡμέρες. Πολλοὶ ὑθροὶ (προπάντως Ἀράχνες καὶ ληστικές μυῖγες) εἶναι ὑπεύθυνοι γιὰ τὸ ὅτι τὰ μυρμήγκια δὲν ζοῦν ὅπως στὸ ἐργαστήριό πολλὰ χρόνια. Ἀπὸ τοὺς πιὸ πάνω αναφερθέντες ἀριθμούς, μπορεῖ κανεὶς νὰ υπολογίσει, πόση τροφή μπορεῖ νὰ φέρῃ ἓνα μυρμήγκι στὴν ἀποικία, στὴν διάρκεια τῆς ζωῆς του. Παράξενα πῶς, ἀλλὰ οἱ υπολογισμένοι ἀριθμοὶ συμφωνοῦν καὶ στά Ἑλληνικά καὶ στά Τυνησιακά μυρμήγκια. Κάθε *Cataglyphis bicolor* μεταφέρει στὴν διάρκεια τῆς ζωῆς του τὸ ἑικοσαπλὸ τοῦ δικοῦ του βάρους στὴν ἀποικία.

9. Κατὰ τὴν διάρκεια τῆς ἀναζήτησης τροφῆς ἔχουν τὰ μυρμήγκια τὸ πρόβλημα νὰ ξεναβροῦν τὴν μικρὴ, ὄχι καὶ τόσο φανερὴ, φωλιά τους, ἀπὸ μεγάλες ἀποστάσεις. Γιὰ προσανατολισμὸ χρησιμοποιοῦν δύο συστήματα. Ἐνα ἄστρονομικὸ σύστημα καὶ ἓνα ἐπίγειο σύστημα. Κατὰ τὸ ἄστρονομικὸ σύστημα μποροῦν νὰ κανονίσουν τὰ μυρμήγκια τὴν κατεύθυνση πρὸς τὴν φωλιά, ἀκόμη καὶ ἂν δὲν ὑπάρχουν σημάδια στὴν γῆ. Τὸ σύστημα ἐργάζεται πάντως ὄχι μὲ ἀκρίβεια. Εάν ὑπάρχουν σημάδια στὴν γῆ, τότε ἀνέρχεται ἡ ἀκρίβεια τοῦ προσανατολισμοῦ.

10. Ὁ προσανατολισμὸς μὲ τὴν βοήθεια σημαδιῶν πάνω στὴν γῆ θὰ ἐξετασθεῖ πειραματικά. Χρησιμοποιοῦμε γι' αὐτὸ τὸν σκοπὸ μαῦρους κυλίνδρους, οἱ ὁποῖοι δείχνουν στά μυρμήγκια τὸν δρόμο πρὸς τὴν φωλιά. Τὰ ἀποτελέσματα πολλῶν πειραμάτων δείχνουν τὰ ἑξῆς συμπεράσματα. Τὸ μυρμήγκι «Βγάζει μία φωτογραφία» τῆς περιοχῆς γύρω ἀπὸ τὴν φωλιά του. Αὐτὴν τὴν εἰκόνα τὴν κρατᾷ στὴ μνήμη του κατὰ τὴν διάρκεια τῆς ἀναζήτησης τροφῆς. Ὅταν ἐπιστρέφει ἀργότερα στὴν φωλιά του προσπαθεῖ νὰ φέρῃ σε ἀκάλυψη τὴν εἰκόνα τῆς μνήμης του μὲ τὴν πραγματικὴ εἰκόνα. Εάν τὸ μυρμήγκι δεῖ τὰ σημάδια πάνω στὴν γῆ ἀπὸ μία ἄλλη προοπτικὴ, τότε δὲν βρίσκει τὸν δρόμο πρὸς τὴν φωλιά. Τὸ μυρμήγκι κατέχει ἓνα γεωγραφικὸ χάρτη γύρω ἀπὸ τὴν φωλιά του, ὅπως ἓνας ἀνθρώπινος προσανατολιστής.

Εὐχαριστοῦμε θερμὰ τοὺς Ἑλληνες καὶ Ἀραβες φίλους, χωρὶς τὴν βοήθεια τῶν ὁποίων δὲν θὰ ἦταν δυνατὴ αὐτὴ ἡ ἐργασία.

VIII. References

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