

The coexistence of two large-sized thermophilic desert ants: the question of niche differentiation in *Cataglyphis bicolor* and *Cataglyphis mauritanica* (Hymenoptera: Formicidae)

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Abstract

In the Tunisian highland steppes the desert ant species *Cataglyphis bicolor* (FABRICIUS, 1793) and *C. mauritanica* (EMERY, 1906) share common microhabitat preferences. Endowed with equally sized workers they exhibit the same daily activity patterns within equally sized foraging areas, where they scavenge for the same type and size of food items. Neither do they establish food territories nor do their foragers avoid the vicinity of neighbouring nests, be they conspecific or allospecific. Due to this strong overlap of the ecological niches of *C. bicolor* and *C. mauritanica* the question arises whether the coexistence of the two species is a stable one, or whether it just reflects a temporary episode within a colonization process recurring time and again in instable environments.

Key words: *Cataglyphis*, competition, niche differentiation

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Introduction

Competition is one of the strongest driving forces of evolutionary processes. As often stated, in a stable environment two coexisting species should exhibit at least small differences in resource exploitation, i.e., occupy different niches (GAUSE 1934, HARDIN 1960, MAY 1976a). It is only in the absence of competition, e.g., if there is a surplus of food or breeding places that the niches of coexisting organisms can overlap (MAY 1976b). This "competitive exclusion principle" has been criticized as being not testable and based on circular arguments: "If the species exist, then they are sufficiently different; if they do not coexist, then clearly they are too similar" (KEDDY 1989). The focus of the present study on niche separation in two sympatric species of desert ants, *Cataglyphis bicolor* (FABRICIUS, 1793) and *Cataglyphis mauritanica* (EMERY, 1906), is to demonstrate to what extent the competitive interactions of the two sympatric species depend on differences in space use, foraging time, and food resources. The result will be that on the basis of these parameters, i.e., nest site and foraging ecological parameters, alone the coexistence of the two species cannot be explained.

Studies of ant populations have largely contributed to our understanding of interspecific niche separation. They have provided ample evidence that competition between different species correlates with the degree of ecological similarity between the species, because two species using the same limited resources, such as food or nest sites, compete on a higher level than species with different necessities (BERNSTEIN 1979, SEIFERT 1987, HÖLLDOBLER & WILSON 1990). The differences between closely related sympatric species increase when both species are common and belong to the same feeding guild (DELAGE 1968, BERNSTEIN 1974, CHEW & CHEW 1980). Among the factors that differentiate between such closely related species of ants are body size and its correlation with prey

size (HÖLLDOBLER 1976, HANSEN 1978, CHEW & DE VITA 1980, RETANA & CERDÁ 1994, WETTERER 1995), colony size (FOITZIK & HEINZE 1999), patterns of nest site distribution (LEVINGS & FRANKS 1982, CUSHMAN & al. 1988), modes of territory defence (HÖLLDOBLER & LUMSDEN 1980), and often most conspicuously temporal avoidance by adopting different activity rhythms (BRIESE & MACAULEY 1980, KLOTZ 1984, BESTELMEYER 2000).

Nevertheless, there are some examples that ecologically similar species of ants (same food guild, equal body size, equal activity rhythms) do in fact coexist. This coexistence is explained as the result of changing environments or of different susceptibilities to parasites and predators (FEENER 1981, RETANA & al. 1991).

The present study focuses on the interspecific and intraspecific competition in two sympatric formicine desert ants, *Cataglyphis bicolor* and *Cataglyphis mauritanica*. Members of both species are common, equally sized scavengers sharing their habitats in the highland and lowland steppes of central Tunisia (WEHNER & al. 1994). All *Cataglyphis* species belonging to the *C. bicolor* species group and the *C. altisquamis* species group (as *C. mauritanica* does) forage individually for dead arthropods (HARKNESS & WEHNER 1977, WEHNER & al. 1983, RETANA & al. 1986, CERDÁ & al. 1989) and do not exhibit any kind of pheromone-mediated recruitment (WEHNER 1987). In many parts of Tunisia, *C. bicolor* lives sympatrically with the smaller-sized *C. albicans* ROGER (1859). Usually differently sized foragers prefer differently sized food items (for seed-harvesting ants see, e.g., DAVIDSON 1977a, b, HANSEN 1978, WHITFORD 1978a, 1978b, CHEW & DE VITA 1980), and SCHMID-HEMPPEL (1983) has shown that this kind of food-size segregation is the basis of the coexistence of *C. bicolor* and *C. albicans*. By the same token, the coexistence of two equally sized and closely related ants

of the same food guild, as it occurs in *C. bicolor* and *C. mauritanica*, should imply a high level of competition between the two species and thus should have led to niche differentiation.

In the present account we address this question of niche differentiation in *C. bicolor* and *C. mauritanica*. In particular we ask, whether both species differ in morphometrics or in the spatial and temporal use of their microhabitat. Knowing that both species forage individually for dead arthropods we still test for differences in their diet concerning to sizes of the food items and species composition. We further inquire whether competition, both interspecific and intraspecific, results in an overdispersed nest-site distribution or in the spatial avoidance of foragers from neighbouring nests. Finally, if food availability were a limiting resource in these coexisting populations we would expect some kind of inhibitory effect to occur between the forager forces of adjacent conspecific and allospecific nests.

Material and Methods

All experiments were performed 10 km to the southwest of Kasserine (central Tunisia), where *C. mauritanica* and *C. bicolor* occur sympatrically (see WEHNER & al. 1994: fig. 10). The research area (N 35° 07', E 08° 44') belongs to the Tunisian high altitude steppe, which receives about 470 mm of annual precipitation and is characterized by halfa grass (WALTER & LIETH 1967, FRANKENBERG 1979). The sandy and stony area is continuously but sparsely (< 10 %) covered with vegetation (*Stipa tenacissima* [L., 1758], *Peganum harmala* [LINNAEUS, 1758], several Poaceae). Medium annual temperatures amount to only 15 °C (WALTER & LIETH 1967), but during our experimental period maximum soil-surface temperature reached 42 °C (in early July).

Morphometrics

Both *C. bicolor* and *C. mauritanica* represent large-sized species of the genus *Cataglyphis*. Morphometrical data (head width measured in dorsal view just in front of anterior eye margin; length of the hind-leg tibia) were obtained from 500 specimens per species. Two colonies of each species, i.e. four colonies in total, were excavated and the individuals preserved in 70 % ethanol. On a random basis, 250 specimens per colony were taken from these samples by the following procedure: the members of each colony were subdivided into five glass vials. After stirring the samples, 50 workers were taken from each vial for the measurements. The Mann-Whitney test was used to compare interspecific samples. In addition we compared species specific and nest specific differences by applying Dunn's Multiple Comparison test.

Food preferences

In an area where several nests of both species occurred in close distances foragers carrying a food item were caught (*C. bicolor*: 102, *C. mauritanica*: 101). Foragers and food were stored in absolute ethanol and later dried in a desiccator for six days until the mass of ten focus ants remained stable for one day. For each forager we calculated the head width (which in both species is linear correlated with the forager's dry weight [data not shown]) and for its according food item we measured the dry

mass (Mettler AM 50, accuracy: 0.1 mg) and the length of its maximum extension.

Microhabitat

The herb *Peganum harmala* is the most abundant plant species in the research area. It might provide the foraging ants with shady places. Local accumulations of this plant also might be an indicator for small-scale differences in chemical soil structure or soil humidity. We therefore recorded the numbers of this plant in circular areas (radius: 10 m) around the nest entrances and compared the data for 10 *C. bicolor* nests and 10 *C. mauritanica* nests (Mann-Whitney test). Even though the research area is homogeneously and sparsely covered with vegetation (see above), we tested whether nesting sites of *C. bicolor* and *C. mauritanica* differed in their physical soil structure. The hardness of the soil was analysed by a metal cylinder (mass: 2 kg) falling along a vertical rod from 1.5 m height onto a nail provided with a centimetre scale. The depth of the penetrating nail depended on the hardness of the soil. To determine the hardness of the upper soil layer, measurements started with the tip of the nail positioned on the ground. To obtain information about the lower soil layers, the nail was hammered 12 cm into the ground, and then the test was repeated. Upper and lower soil structures were analysed for 22 *C. mauritanica* nests and 13 *C. bicolor* nests. At each nest four measurements were taken at the corners of a square (side length: 30 cm) centred about the nest entrance. Mean penetrations at the surface and at 12 cm depth were compared for both species by using the Mann-Whitney test.

Daily activity

Foragers leaving the nest were recorded by a photo-sensor device that counted only the leaving but not the returning ants. By simultaneously using 6 of these devices we were able to measure the daily activity of 6 nests (3 nests of each species) on the very same day. In total, measurements were taken at 12 *C. mauritanica* and 12 *C. bicolor* nests.

In addition we labelled 18 foragers of *C. bicolor* and 15 foragers of *C. mauritanica* individually, and recorded the number of foraging runs per ant and day.

Competition

Nest distribution

All nests of the two species were mapped within an area of 250 m × 350 m (56 nests of *C. mauritanica* and 24 nests of *C. bicolor*). We used the map to perform nearest-neighbour analyses (CLARK & EVANS 1954), in order to test whether interspecific or intraspecific competition has led to overdispersed nest-site distributions. The nearest-neighbour analysis provides a distributional index *R*, which can range from 0 (perfect aggregation) to 2.15 (perfect spacing with a hexagonal distribution). A value of 1 is indicative of a random distribution.

Foraging areas of colonies and foraging ranges of individuals

In order to be able to record the spatial layout of the ants' foraging activities we painted grids of white lines around the nest entrances. Each grid consisted of 6 concentric circles (radii: 5, 10, 15, 20, 25 and 30 m) subdivided into

8 (n = 5 focus nests) or 16 (n = 8 focus nests) sectors. On day zero all foragers of a focus nest were labelled with a nest specific colour dot. The following day we scanned the grid at 1-hour intervals from 8:00 to 17:00 (standard local time) for marked foragers and recorded their positions within the segments of the grid. Ants digging at the nest entrance were not counted as foragers and therefore excluded from the analysis. The scanning procedure performed by two observers took 18 - 20 min. for the whole grid (scanning rate about 1.2 m²/s).

In addition, for each focus nest the mean values of scanned ants per day were computed in sectors with and without neighbouring nests. The Wilcoxon-Signed-Ranks test was used to test for differences between the two data sets. These tests were performed separately for conspecific neighbours and for allospecific neighbours.

Activity and foraging success of 9 non-neighbouring focus nests of *C. mauritanica* were recorded on two consecutive days. On both days the numbers of ants leaving the nest, and the numbers of ants returning to the nest with food and without food were recorded within 20 min. periods at the same time of day (always p.m.). On the second day all ants from nests that were less than 40 m apart from the focus nests were prevented from foraging by closing the nest entrances with sand mounds. These nest closures were checked continuously and, if necessary, re-established until the end of the recording period. The control (first-day) data and the (second-day) data of the competition-exclusion experiments (number of ants leaving the focus nest, number of prey items, and foraging efficiency, i.e., the number of prey items brought into the nest divided by the number of returning ants) were compared by using the Wilcoxon-Signed-Ranks test.

Results

Morphometrics

Cataglyphis bicolor and *C. mauritanica* can be distinguished easily by the shape of their petiole: while the petiole of *C. bicolor* (and all other *Cataglyphis* belonging to the *bicolor* species group) is nodiform, that of *C. mauritanica* is cuneiform which prevents the ants from lifting the gaster as *C. bicolor* does. Here we asked the question, whether both species differ also in other morphometrical parameters that could account for different foraging abilities. We focused on head width, which at least in *C. bicolor* and *C. albicans* is correlated with prey size (SCHMID-HEMPEL 1983), and on leg length (length of the hind-leg tibia), which influences the ants' speed and ability to stilt above the hot substrate (WEHNER 1983, CERDÁ 2001). We excavated 2 *C. bicolor* nests (1054 and 867 ants per nest) and 2 *C. mauritanica* nests (1170 and 723 ants per nest) and measured head width and length of the hind leg tibia for 250 randomly taken ants of each nest. Both *C. bicolor* and *C. mauritanica* are monomorphic species without any morphological caste specialization as shown by the linear correlation of both measured parameters in logarithmic scale (Fig. 1, central graph). They have an extensive overlap in size of their workers with a difference in head width (Fig. 1, lower inset: *C. bicolor*: 1.72 ± 0.40 mm, *C. mauritanica*: 1.61 ± 0.50 mm; Mann-Whitney test, n = 1000, p < 0.001) and no difference in the length of tibia (Fig. 1, left-hand inset: *C. bicolor*: 3.35 ± 0.79 mm, *C. mauritanica*: 3.28 ± 1.02 mm; Mann-Whitney test, n =

1000, p = 0.17). However, when we tested not only for interspecific differences but also for intraspecific differences between the nests, intraspecific differences sometimes exceeded the interspecific ones (*C. bicolor* nest 1 vs. *C. bicolor* nest 2, $p_{\text{head width}} < 0.001$, $p_{\text{tibia length}} < 0.001$; *C. bicolor* nest 1 vs. *C. mauritanica* nest 2, $p_{\text{head width}} > 0.05$, $p_{\text{tibia length}} > 0.05$, Dunn's Multiple Comparison test). Hence, coexistence does not lead to competition avoidance by means of different species-specific worker sizes. Noteworthy the weak but significant difference in the head width between *C. bicolor* and *C. mauritanica* ants collected from inside the nests (Fig. 1, lower inset) disappeared when only food carrying foragers were taken into consideration (Fig. 2, lower inset). Therefore not only the distribution of worker sizes overlap widely but the foraging cohorts of both species are even more alike with a head width in *C. bicolor* foragers of 2.15 ± 0.34 mm and in *C. mauritanica* foragers of 2.14 ± 0.29 mm. (*C. bicolor* foragers vs. *C. mauritanica* foragers, Mann-Whitney test: p = 0.7). The equal sizes of the foragers directly lead to the question whether there are any species-specific food preferences at all.

Food preferences

Cataglyphis ants usually forage for dead arthropods. Due to the extensively overlapping worker sizes in *C. bicolor* and *C. mauritanica* significant differences in the ants' prey sizes were not to be expected. The analysis of about 100 food items collected in either species simultaneously and within the same area confirmed this expectation. There was a wide and completely overlapping distribution of the sizes of the food items with respect to both the dry weights and the lengths of the items. Neither parameter was correlated with the head widths of the foragers (Fig. 2, top graphs). Furthermore, we could not observe any differences in prey qualities (Tab. 1). In conclusion the composition of the food intake into the colony seems to depend completely on food availability.

Microhabitat

Whenever *C. bicolor* shares its habitat with *C. savignyi* (DUFOUR, 1862) – another ant of the *C. bicolor* species group – there is a clear-cut nest site specialization with *C. bicolor* nests being more closely located to food providing plants (DIETRICH & WEHNER 2003). Here, we asked whether the same is true for sympatric occurrence of *C. bicolor* and *C. mauritanica*. Although the actual study site is more homogenous and contains no oases or fruit gardens, as the sympatric area of *C. bicolor* and *C. savignyi* does, we found some local accumulations of the plant *Peganum harmala*, which could provide shade and honeydew and which could also indicate small-scale soil differences. Nevertheless, we could not detect any differences in the number of plants around the nests (numbers of *Peganum harmala* within a radius of 10 m: *C. bicolor*: 70 ± 68 , *C. mauritanica*: 50 ± 36 , n = 10 nests of each species, Mann-Whitney test: p = 0.35). In addition, by testing the hardness of the soil with a special device (see Materials), the depth of the penetration of a standard-size nail did not differ in both species irrespective whether the upper or lower soil structure were tested (upper soil: *C. mauritanica*: 7.6 ± 1.1 cm, n = 22, *C. bicolor*: 7.3 ± 1.9 cm, n = 13, Mann-Whitney test: p = 0.85; lower soil: *C. mauritanica*: $2.2 \pm$

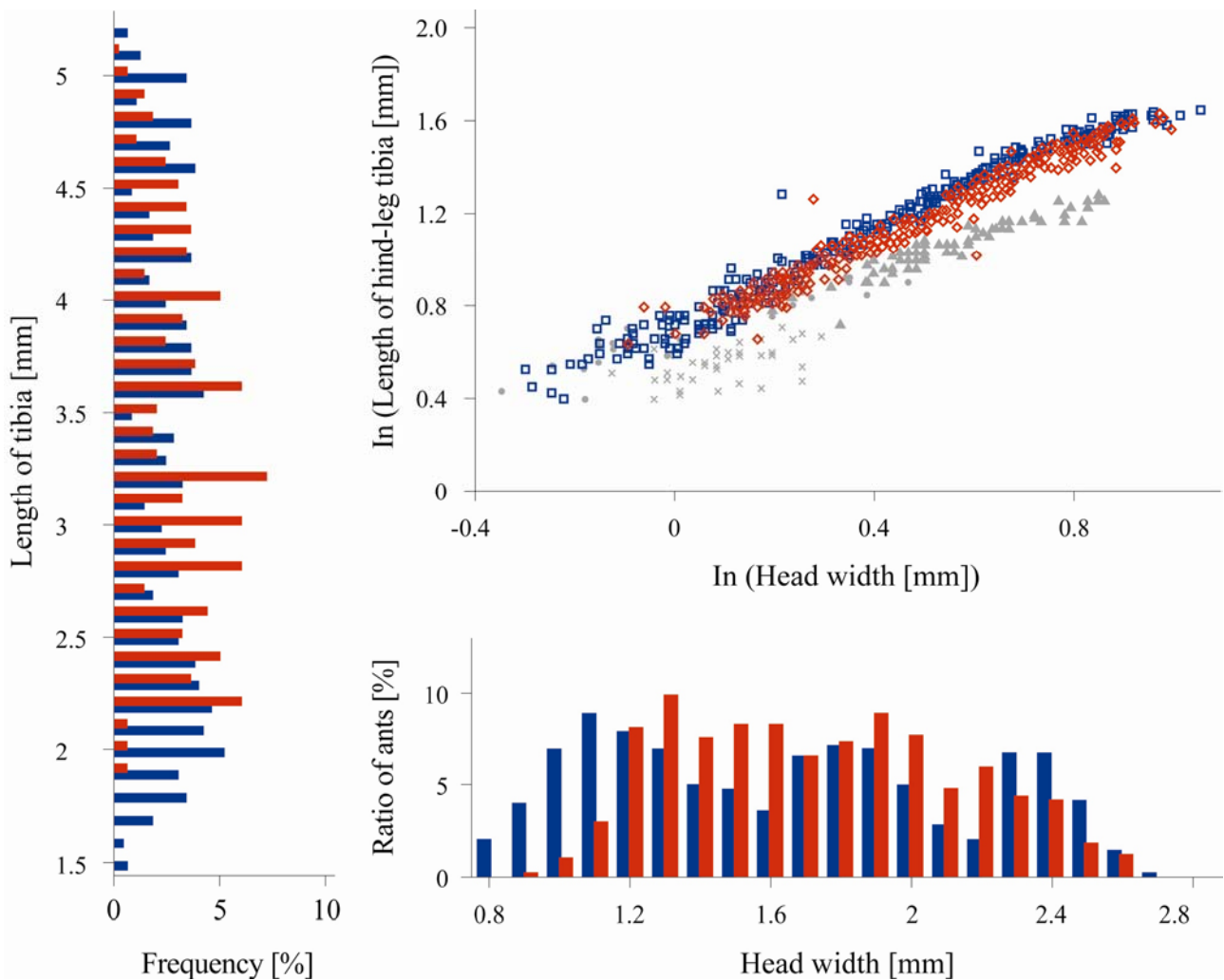


Fig. 1: Central graph: correlation between head width and the length of the hind-leg tibia (double logarithmic plot). Blue squares: *C. mauritanica*, blue regression line: $y = 1.02x + 0.7$, $R^2 = 0.98$; red squares: *C. bicolor*, red regression line: $y = 1.00x + 0.67$, $R^2 = 0.96$. ANCOVA revealed differences in slope ($F = 11.2$, $p < 0.001$) and intercept ($F = 138.4$, $p < 0.001$) when head width was taken as covariate. Data from *C. fortis* (grey triangles), *C. albicans* (grey crosses) and *C. cursor* (grey circles) are given in addition, in order to illustrate the usually high interspecific variability within the genus *Cataglyphis*. Lower inset: frequency distribution of the tibia lengths of the hind legs in *C. bicolor* (red bars, $n = 500$) and *C. mauritanica* (blue bars, $n = 500$). Left-hand inset: frequency distribution of the head widths in *C. bicolor* (red bars, $n = 500$) and *C. mauritanica* (blue bars $n = 500$).

0.7 cm, *C. bicolor*: 2.2 ± 1.1 cm, Mann-Whitney test: $p = 0.95$). Hence, coexistence cannot be explained by the use of different microhabitats.

Daily activity

In desert ant assemblages subordinate species often forage at high temperatures close to their physiological thermal limits (CERDÁ 2001). Although both *C. bicolor* and *C. mauritanica* are thermophile and belong to a typical subordinate genus (CERDÁ & al. 1998, CERDÁ 2001), competition could drive the activity peak of a possible lower ranked species closer to the daily thermal maximum. Therefore, we tested whether *C. bicolor* and *C. mauritanica* differ in their daily activity rhythms. At 11 *C. bicolor* nests we detected 699 ± 817 (110 - 2974) departures (exits), whereas 740 ± 543 (141 - 1755) departures were counted at 12 *C. mauritanica* nests. In addition, the count of foraging runs of individual foragers revealed similar activity patterns in both species (*C. bi-*

color: 5.2 ± 1.7 runs per day, $n = 18$, *C. mauritanica*: 4.6 ± 3.7 runs per day, $n = 15$, Whitney-Mann test, $p = 0.27$). Therefore, the similar numbers of automatically detected departures for both species seem to be based on similarly sized forager forces. In this context, it should be pointed out, that this similarity in the size of the forager force is in accord with the total worker forces of the colonies (see Morphometrics section). It is also in accord with our recordings at nests of which all foragers had been labelled (*C. mauritanica*: 141 ± 75 foragers per nest, $n = 10$ nests; *C. bicolor*: 100 ± 11 foragers per nest, $n = 4$ nests). Returning to the question of possible temporal shifts of foraging activity as a strategy of avoiding competition between the two coexisting *Cataglyphis* species, we can refer to Fig. 3 and conclude that the two species exhibited similar daily activities. There were no significant activity peaks during the course of the day. Clearly, temporal avoidance cannot account for the coexistence of *C. bicolor* and *C. mauritanica*.

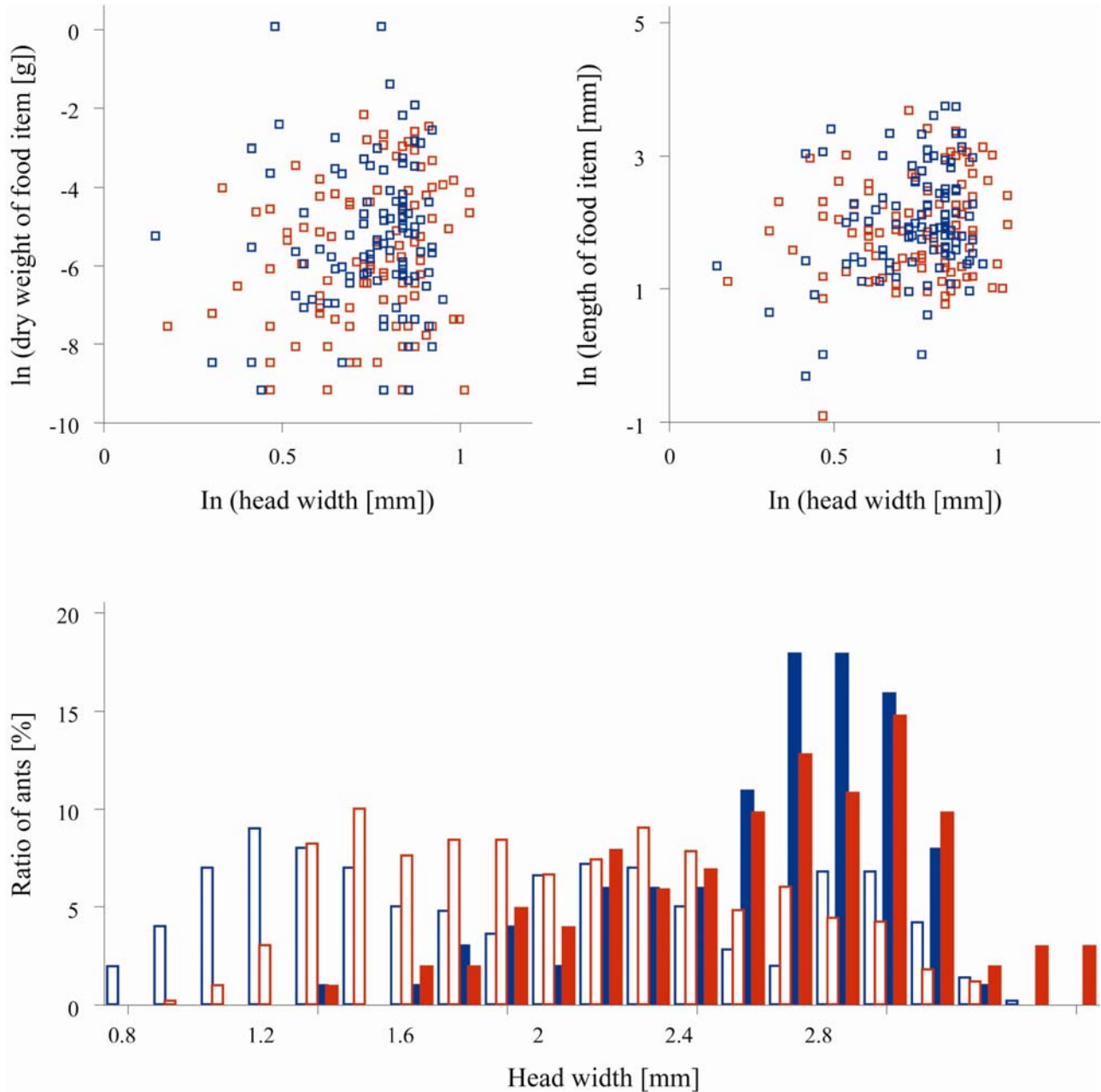


Fig. 2: Top graphs: Relationship between head width of the foragers and the size of the food items retrieved by them (double logarithmic plots; blue squares: *C. mauritanica*, red squares: *C. bicolor*; left: dry weight of food item (*C. m.*: correlation coefficient $r^2 = 0.004$, $p > 0.05$; *C. b.*: $r^2 = 0.02$, $p > 0.05$), right: length of the maximum linear extension of food item (*C. m.*: $r^2 = 0.03$, $p > 0.05$; *C. b.*: $r^2 = 0.02$, $p > 0.05$). Lower inset: frequency distribution of the head widths of the foragers captured outside the nest (blue bars: *C. mauritanica*, $n = 101$, red bars: *C. bicolor*, $n = 102$) and of individuals taken from entire colonies (two colonies in either species; open blue bars: *C. mauritanica*, open red bars: *C. bicolor*).

Tab. 1: Food items collected by *C. bicolor* and *C. mauritanica*. SPA: small parts of arthropods, UI: unidentified items, PM: plant material. χ^2 : $p = 0.95$ with SPA, UI and PM being excluded from the analysis.

Species	Hymenoptera	Orthoptera	Coleoptera	Diptera	Hemiptera	Araneae	SPA	UI	PM	Σ
<i>C. bicolor</i>	24	12	6	8	9	4	38	0	1	102
<i>C. mauritanica</i>	27	12	6	4	12	3	29	6	2	101

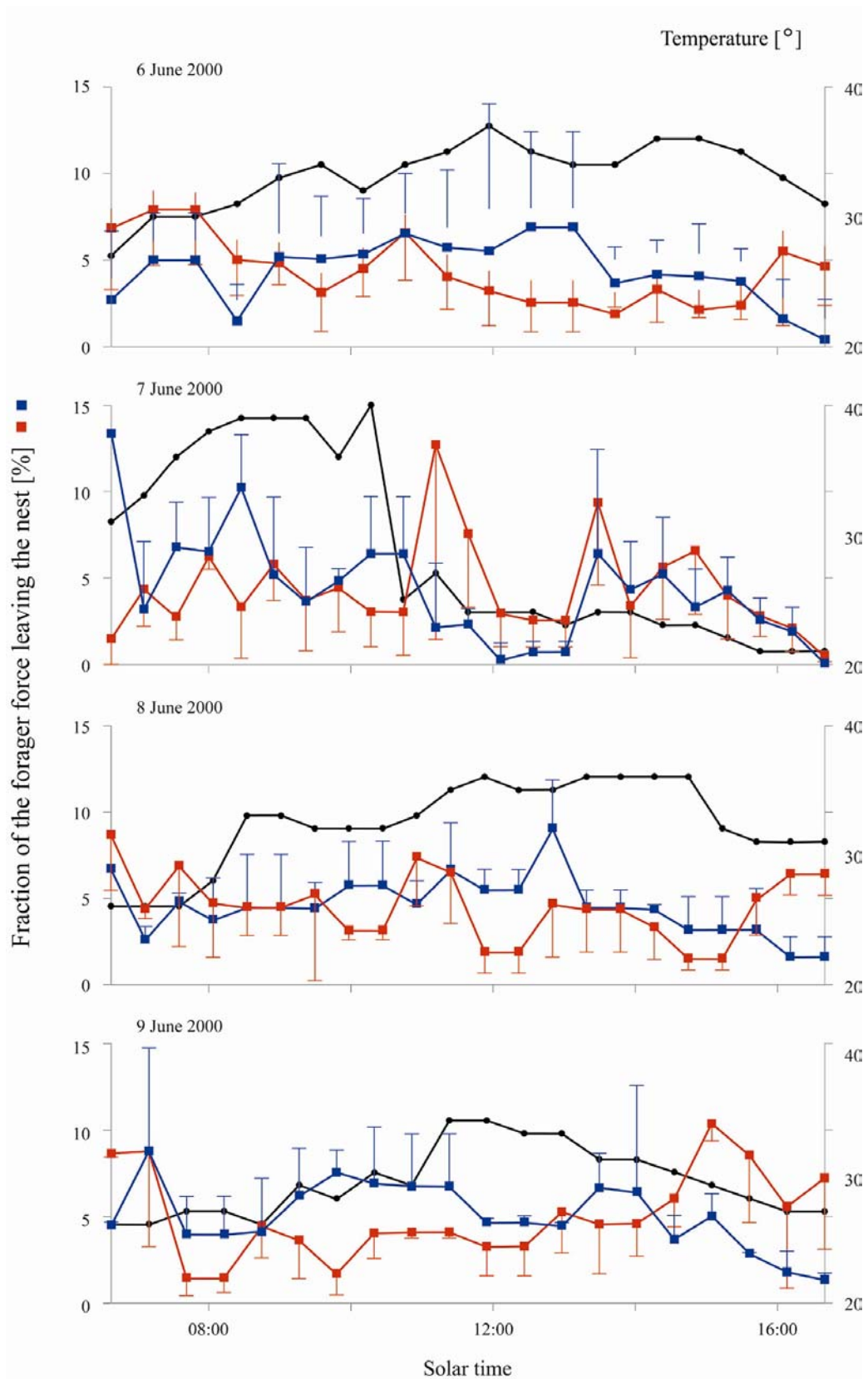


Fig. 3: Daily foraging patterns of *C. mauritanica* nests (blue squares, $n = 12$ with 3 nests measured per day) and *C. bicolor* nests (red squares, $n = 12$ with 3 nests measured per day) on four consecutive days (6 June 2000 - 9 June 2000). The lines depict the fraction of the entire foraging force in each 30-min interval of the day (averaged over the three conspecific nests per day). The error bars depict the standard deviation. Foragers leaving the nests were automatically counted by a photo-sensor device, while returning ants were not counted. The black line represents the temperature at 1 cm above ground. The black bar in the second graph indicates the duration of a period of continuous rainfall.

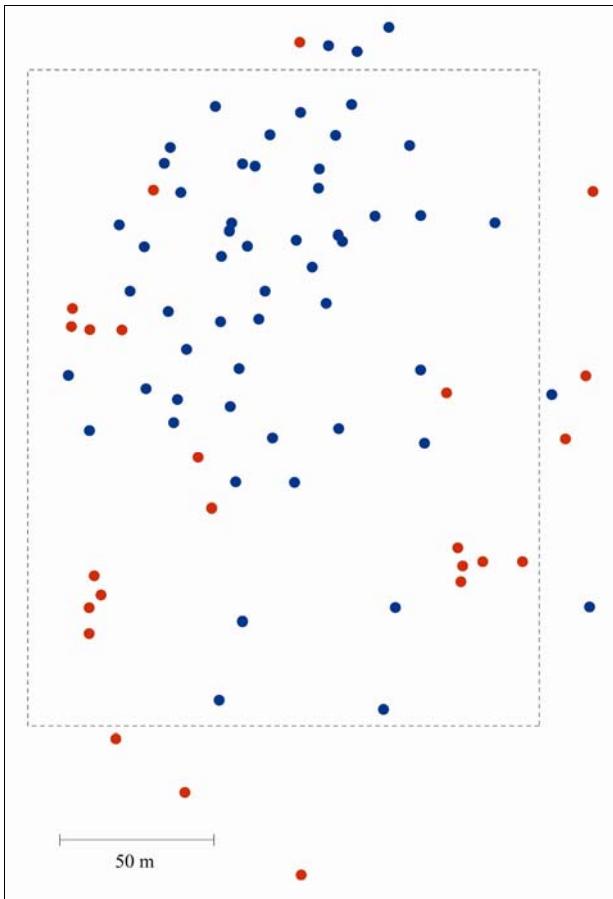


Fig. 4: Distribution of nests within the test area. Red circles: *C. bicolor* nests; blue circles: *C. mauritanica* nests. Continuous line: total test area; dashed line: core area exhibiting the highest nest density.

In conclusion, we could not detect any niche differentiation parameters between the two coexisting species with respect to either morphometrics, or food and microhabitat preferences, or temporal activity patterns. Nevertheless, does foraging competition, if it occurs at all, influence the spatial habitat use of both species, as it might be reflected in the distribution of nesting sites within the sympatric zone and/or in the distribution of the forager forces around the nests?

Nearest-neighbour analysis

A total of 79 nests (24 *C. bicolor* nests and 55 *C. mauritanica* nests) occurred within our 8.8-ha large test area (Fig. 4). Despite the apparently homogenous vegetation and soil structure characterizing this area, 85 per cent of the nests were located in only 37 per cent (3.5 ha) of the area. Hence nearest-neighbour analyses were performed for both the entire area (8.8 ha, $9.0 \text{ nests} \times \text{ha}^{-1}$) and the smaller "core area" (3.5 ha) exhibiting the highest nest density ($19.1 \text{ nests} \times \text{ha}^{-1}$).

These analyses (parameter R, Tab. 2) provide information about the degree to which the observed distribution of nests departs from a random one. The *C. mauritanica* nests as well as the nests of both species together were located in clusters within the whole area, but randomly distributed within the core area, while *C. bicolor*

Tab. 2: Distribution of *Cataglyphis mauritanica* nests, *C. bicolor* nests and the nests of both species combined. *C. m.*: *Cataglyphis mauritanica*, *C. b.*: *Cataglyphis bicolor*, b. s.: both species, N: number of nests, ρ : nest density [nests/m²], D_r : expected mean distance to the nearest neighbour in a large random distribution with density ρ , D: measured mean distance to the nearest neighbour. The parameter R describes the type of distribution (R = 1, random distribution; R = 0, maximum aggregation; R = 2.15, maximum spacing). The asterisks ** indicate that the zero hypothesis R = 1 can be rejected by $p < 0.01$; n.s. means $p > 0.05$.

	Total research area			Core area		
	<i>C. m.</i>	<i>C. b.</i>	b. s.	<i>C. m.</i>	<i>C. b.</i>	b. s.
N	55	24	79	50	17	67
ρ	0.0006	0.0006	0.0022	0.0015	0.0005	0.002
D_r [m]	19.31	29.48	16.22	12.79	22.01	11.1
D [m]	14.13	19.12	12.08	12.71	11.51	11.34
R	0.73**	0.65**	0.75**	0.98 n.s.	0.52**	1.02 n.s.

nests were distributed in clusters in both the entire and the core area. Hence, if in the coexisting populations of *C. bicolor* and *C. mauritanica* intraspecific or interspecific competition occurred, it had not resulted in a regular spacing of the nests.

Territorial behaviour

Apart from nest-site distributions, competition could result in establishing foraging territories (direct competition) or in the foragers avoiding the vicinity of neighbouring nests, because neighbours might have already depleted their surrounding foraging area (scramble competition). Therefore we investigated the space use patterns of the forager forces of individual nests by marking foragers of 14 nests with nest-specific colours and repeatedly scanning the foragers' positions within a circular grid (diameter 60 m) painted around the nest entrances. The positions of 969 *C. mauritanica* foragers from 10 nests and of 305 *C. bicolor* foragers from 4 nests were recorded (Fig. 5A). About 60 to 70 per cent of the foragers of either species were found closer than 10 m from their nest, while there were less than 10 per cent searching in more than 22 m distance from their nests. If one defines the foraging range of a colony as a circular area to which the whole forager force devotes 90 per cent of its total search time (WEHNER & al. 1983), the radius of this circle is 22 m in either species (Fig. 5B) and hence much larger than the mean distance between neighbouring nests of *C. bicolor* and *C. mauritanica* (12.1 m in the entire area and 11.3 in the core area, Tab. 2). This extensive overlap of neighbouring foraging areas immediately stimulates the question, whether *Cataglyphis* foragers

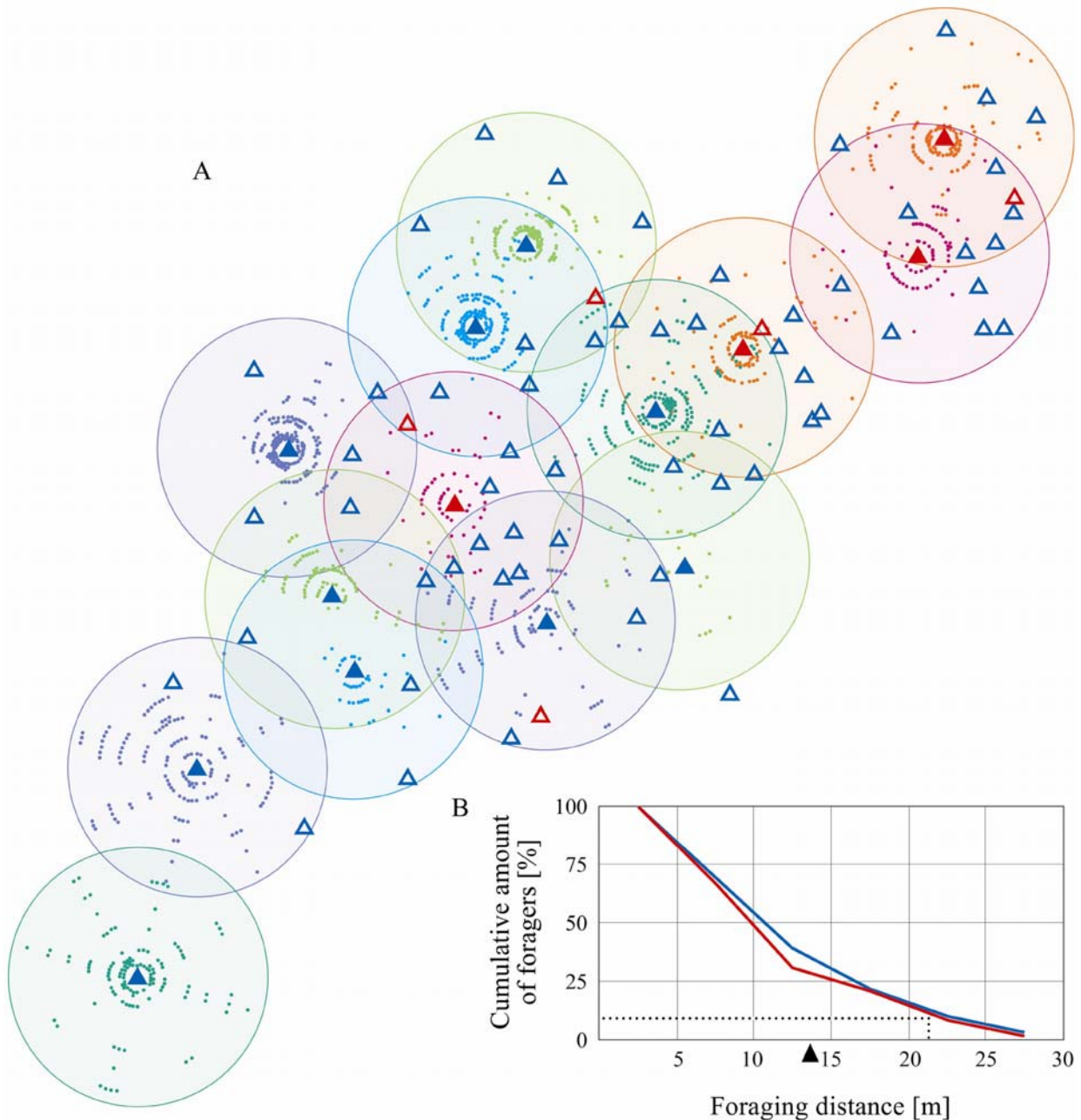


Fig. 5: (A) Spatial distribution of the foraging activities of 14 focus nests (filled blue triangles: *C. mauritanica*; filled red triangles: *C. bicolor*). The coloured dots depict the positions of foragers of each focus nest during a one-day recording period (for recording procedure see Methods). Open triangles indicate the locations of *Cataglyphis* nests lying at a radial distance of ≤ 30 m from each focus nest, i.e. within the coloured circle drawn around each focus nest. (B) Cumulative search frequency as a function of the distance from the nest. Blue line: *C. mauritanica* (n = 10 nests with 969 observed ants); red line: *C. bicolor* (n = 4 nests with 303 observed ants); error bars depict the standard deviation. The dotted line signatures mark the distance from the nest up to which 90 % of the total amount of foragers were found. The black arrow denotes the mean distance to the nearest neighbouring nest.

avoid the vicinity of neighbouring *Cataglyphis* nests. Therefore, in the vicinities of several focus nests we mapped the positions of all neighbouring nests within the grid and tested if these neighbours influenced the search density of the focus colony. Within the grids of the 10 *C. mauritanica* focus nests we mapped a total of 38 *C. mauritanica* and 4 *C. bicolor* neighbouring nests. The 4 *C. bicolor* focus nests had a total of 39 *C. mauritanica* and 4 *C. bicolor* neighbouring nests. In either species, there

was no decrease in the foraging density in the vicinity of neighbouring conspecific or allospecific *Cataglyphis* nests (Fig. 6). Single foragers were even observed to forage less than 1 m away from neighbouring conspecific and allospecific nests without causing any aggressive attacks. In conclusion, competition in the coexisting populations of *C. bicolor* and *C. mauritanica* causes neither any regular spacing of neighbouring nests nor any territoriality or spatial avoidance in the foraging behaviour of individual ants.

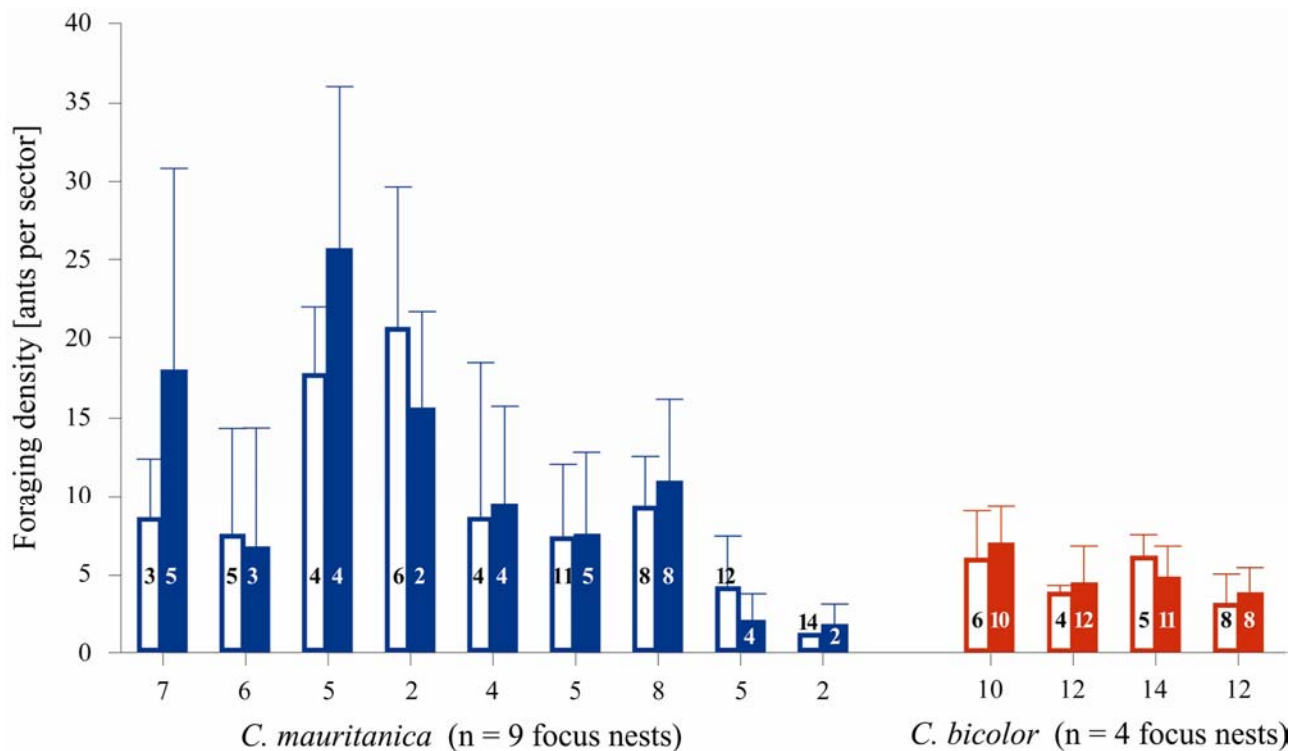


Fig. 6: Influence of neighbouring *C. mauritanica* nests on the spatial distribution of foraging activities of *C. mauritanica* nests (blue) and *C. bicolor* nests (red). Open bars: mean numbers (+ SD) of foragers recorded in sectors devoid of neighbouring nests; filled bars: mean numbers (+ SD) of foragers in sectors containing neighbouring nests. The numbers within the bars depict the numbers of sectors around each focus nest that did or did not contain neighbouring nests (with a total number of 8 or 16 sectors per nest, depending on the sectioning of the grid). Italic numbers below the bars depict the total number of neighbouring nests of each focus nest. The numbers of foragers did not differ between sectors with or without neighbouring nests (Wilcoxon Signed Ranks test: *C. mauritanica*, $p = 0.44$; *C. bicolor*, $p = 0.70$).

Finally we tested whether food is a limited resource at all. We excluded nests from foraging and recorded whether this exclusion of competition affected the foraging activity and foraging efficiency of undisturbed *C. mauritanica* nests. The experiment was run with 9 focus nests. In total 50 neighbouring nests (2 - 10 nests within a radial distance of 40 m of each focus nest) were prevented from foraging. We could not observe any differences in the number of prey items collected (10 ± 7 food items with active neighbours vs. 7 ± 4 with excluded neighbours, Wilcoxon Signed Ranks test: $p = 0.29$) and in the foraging efficiency of the workers between the two situations ($15 \pm 8\%$ successful foragers with active neighbours vs. $12 \pm 7\%$ with excluded neighbours, $p = 0.86$). Contrary to the hypothesis that closing adjacent nests increases the foraging activity of a focus nest, the number of ants in fact decreased when the neighbours were prevented from foraging (62 ± 25 nest leaving ants with active neighbours vs. 39 ± 14 with excluded neighbours, $p < 0.05$).

In conclusion, in coexisting populations of *C. bicolor* and *C. mauritanica* intraspecific and interspecific competition, if it occurred at all, does not lead either to an isoform (overdispersed) spacing of the nests or to the establishment of foraging territories and any other kind of spatial foraging avoidance. Finally food does not seem to be a limiting factor (at least during early summer, when our experiments were performed).

Discussion

Ecological similarity of coexisting species and the concept of niche differentiation

As the data presented in this study show, the two sympatric North African species of individually foraging desert ants, *Cataglyphis bicolor* and *C. mauritanica*, do not only share the same morphological characteristics that might be influential in their foraging abilities (head width and leg length, Fig. 1), but also forage for same sized food items (Fig. 2) and overlap widely in their microhabitat preferences, their daily activity (Fig. 3), and the spatial use of their foraging area (Fig. 5).

Coexistence of ecologically similar ant species is not as uncommon as expected due to GAUSE's principle (1934). PONTIN (1961, 1963) challenges this principle on the basis of his observation that *Lasius niger* (LINNAEUS, 1758) and *L. flavus* (FABRICIUS, 1782) persistently coexist in spite of their overlapping ecological requirements. He concludes that regulating factors others than ecological similarity might be important for stabilizing the coexistence of these two species. However, SEIFERT (1987) could show that both species differ in their habitat use with *L. niger* foraging mainly above ground and *L. flavus* being specialized on keeping subterranean aphids. RETANA & al. (1992) mention low population density and different susceptibility to parasites as possible effects regulat-

ing coexistence. FEENER (1981) proved the stabilizing effect of *Apocephalus* flies parasitizing on major workers of *Pheidole dentata* MAYR, 1855), but not on workers of its sympatric competitor *Solenopsis texana* EMERY, 1895, as being indirect competition. Nevertheless, the large amount of studies addressing problems of niche differentiation in coexisting species of ants clearly raises the question as to what the potential factors are that establish the coexistence of ecologically similar species (temporal avoidance: STEBAEV & REZNIKOVA 1972, BARONI URBANI & AKTAÇ 1981, HÖLLDOBLER 1981, 1986, KLOTZ 1984; specialization on differently distributed food items: DAVIDSON 1977a, 1977b, HÖLLDOBLER & al. 1978; worker size and polymorphism: HÖLLDOBLER 1976, DAVIDSON 1977a, 1977b, 1978, HANSEN 1978, CHEW & DE VITA 1980, SCHMID-HEMPPEL 1983, RETANA & al. 1992, WETTERER 1995; microhabitat preferences: JOHNSON 2000, DIETRICH & WEHNER 2003). In the present account, however, we can do nothing but demonstrate the remarkable ecological similarity of the two coexisting desert ants *C. bicolor* and *C. mauritanica* by having checked as many parameters of food resource utilization as possible.

Most studies documented differences in at least one parameter whenever coexisting species were compared. For example, coexisting seed-eating ants of the genera *Pogonomyrmex* and *Messor* usually differ either in the size of their workers (and therefore the size of the preferred seeds) or in details of their foraging behaviour (DAVIDSON 1977b, HÖLLDOBLER & al. 1978, RETANA & CERDÁ 1994). A comparison of the sympatric Mediterranean species *Pheidole pallidula* (NYLANDER, 1848) and *Tetramorium semilaeve* ANDRÉ, 1883, revealed wide overlaps in diet, foraging times, and habitat requirements (RETANA & al. 1992). In contrast to the current study, both species belong to distant genera and therefore are not as closely related as *C. bicolor* and *C. mauritanica*, which of course belong to different *Cataglyphis* species groups (AGOSTI 1990). *Pheidole pallidula* and *Tetramorium semilaeve* largely differ in morphometric parameters with the former possessing a major caste and the latter being monomorphic. As emphasized by RETANA & al. (1992) in ecological comparisons of coexisting species one can never be sure that every relevant resource class has been taken into account. Nevertheless, the main result of the present study – the extensive similarities of the sympatric thermophilic scavengers *C. bicolor* and *C. mauritanica* (same microhabitats, equal-sized workers foraging for the same type of food at the same locations and same time of day) – remains surprising.

What are the limiting factors?

HÖLLDOBLER & WILSON (1990) point out that in a population "one factor is usually limiting, and if it were removed, the population would increase until a second factor became limiting, and so on." The number of potential nest sites has been proved to be a limiting factor in ant populations (HERBERS 1986, FOITZIK & HEINZE 1998). We could not find any differences in the microhabitats in which *C. bicolor* and *C. mauritanica* nest. Neither species relies on potentially limited nesting sites such as empty twigs or flat stones (as *Temnothorax* does), but both dig their nests in the same sandy and stony ground with similar plant cover around. Due to the homogeneity of

the area containing a lot of potential nest sites, competition for such sites seems to be unlikely. In addition we never observed nest usurpation as described by CERDÁ & RETANA (1998) for two coexisting subordinate ant species. Next we asked whether food is a limiting resource. Competition for food – be it interspecific or intraspecific – can influence ant populations on different levels. Overdispersed and random nest distribution patterns may result from high and low competition, respectively (CLARK & EVANS 1954, PETAL 1980, RYTI & CASE 1984, 1986). By transplanting *Formica obscuripes* FOREL, 1886, and *Dolichoderus taschenbergi* (MAYR, 1866) colonies into a previously unoccupied area, a large amount of the colonies emigrated when their next neighbour distances were 5 m, while colonies with next neighbour distances of 20 m remained in place (BRADLEY 1972). The *Cataglyphis* nests within the research area exhibited random distributions with a slight tendency towards clustering (Tab. 2). Obviously, intraspecific and interspecific competition between the two *Cataglyphis* species are not strong enough to result in overdispersed nest-site distributions.

Beside colony-site distribution, competition can also affect individual foraging patterns. In their review of foraging strategies in ants, CARROLL & JANZEN (1973) expect "intense competition for scavenged food items." Even though the coexisting *Forelius pruinosus* (ROGER, 1863), *Myrmecocystus depilis* FOREL, 1901, and *M. mimicus* WHEELER, 1906, show wide niche overlap, intense competition leads to interference behaviour in *I. pruinosus*, whose workers prevent the workers of the competing *Myrmecocystus* species from foraging by a chemical repellent (HÖLLDOBLER 1982). Much as *Forelius*, *C. bicolor* and *C. mauritanica* are scavengers for dead arthropods, and hence the two competing species could have evolved similar types of interference behaviour, but none was observed. Furthermore, competition for food could also lead to decreased foraging activities in the vicinity of neighbouring nests, since the neighbours might exhaust the food source around their nests. If the foragers avoided the vicinity of neighbouring nests, merely analyzing the extent of foraging areas would not allow one to discriminate between scramble competition and direct competition (e.g. territory defence). Nevertheless, our finding that foraging activity does not decrease in areas close to neighbouring nests (Fig. 6) speaks against the existence of foraging territories and points towards rather low levels of scramble competition. It should be mentioned, however, that due to the polydomy of at least *C. bicolor* we cannot exclude that neighbouring nests belonged to the same colony. Nevertheless, when all foragers of 14 focus nests were marked with a nest-specific colour, we never observed a marked ant leaving one of the neighbouring nests. Therefore, even if nests belonged to the same colony, their forager forces could be regarded as acting independently. The absence of territoriality in *C. bicolor* and *C. mauritanica* is in accord with the fact that territoriality requires omnipresence of the workers within the territory, to keep strangers out and defence costs low (HÖLLDOBLER & LUMSDEN 1980, JACKSON 1984). We counted 140 ± 75 foragers at the *C. mauritanica* nests (n = 10 nests) and 100 ± 11 foragers at the *C. bicolor* nests (n = 4 nests). These small forager forces do not allow for the omnipresence of workers within the rather large foraging areas (about 1500 m² as calcul-

ated by the radius of the foraging range; Fig. 5). Finally, neither foraging activity nor foraging efficiency of a focus colony increases, when all neighbouring potential competitors are excluded from foraging. This observation again supports our notion that among populations of *C. bicolor* and *C. mauritanica* food competition is low or even absent – at least when food is not limited.

In conclusion, competition for nest sites or food items does not seem to play a major, if any role in stabilizing the coexistence of these sympatric species of desert ant scavengers.

Could the coexistence be explained by different life histories?

When excavating nests we always found only single dealate queens per nest in *C. bicolor*, but up to 7 dealate queens in nests of *C. mauritanica* (at other Tunisian study sites up to 30 such queens were found, WEHNER & al. 1994). In ants the number of queens often corresponds to different nest founding strategies, with monogynous species founding colonies independently after far-reaching mating flights and polygynous species spreading slowly by budding (HÖLLDOBLER & WILSON 1977, KELLER 1991, HEINZE & KELLER 2000). RETANA & al. (1992) discuss different life histories as an alternative factor that might account for the coexistence of similar species. The Tunisian highland and lowland steppes, in which *C. bicolor* and *C. mauritanica* coexist, are erratically used for growing grain. We never found any *Cataglyphis* nests on freshly ploughed land. In case of different colony founding strategies one could hypothesize that small scale coexisting populations of both *Cataglyphis* species are just time frames within a colonization process, in which the freshly ploughed land is first occupied by the fast spreading monogynous species, *C. bicolor*, followed by a slowly budding polygynous one, *C. mauritanica*. In order to reveal such long-term processes, it is necessary to survey colonies at the same study site again. Future investigations will have to show, whether *C. bicolor* and *C. mauritanica* differ not only in the number of their queens but also in their life histories, with *C. bicolor* and *C. mauritanica* being the independent and dependent colony founders, respectively.

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Zusammenfassung

In der tunesischen Hochlandsteppe überlappen sich die Verbreitungsgebiete der beiden Wüstenameisen *Cataglyphis bicolor* und *Cataglyphis mauritanica*. Auch in Gebieten, in denen beide Arten sympatrisch vorkommen, besiedeln sie die gleichen Mikrohabitate. In Nahrungspräferenzen und tageszeitlicher Aktivitätsrhythmik zeigen sie keinerlei Unterschiede. Diese starke Nischenüberlappung in der Ressourcennutzung wirft die Frage auf, ob und inwieweit die Koexistenz beider Arten stabil ist oder einen vorübergehenden Kolonisationsprozess in einem instabilen Habitat darstellt.

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