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Sympatry and allopatry in two desert ant sister species: how do *Cataglyphis bicolor* and *C. savignyi* coexist?

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Abstract Two extremely morphologically similar sister species of desert ants, *Cataglyphis bicolor* and *C. savignyi*, exhibit broadly overlapping distributional ranges within Tunisia. In order to analyse the microhabitats of *C. bicolor* and *C. savignyi* within the sympatric and allopatric areas of both ant species, the plant species located at 113 different nest sites of the two ant species were determined. In the sympatric area, the two species exhibit a clear-cut nest site segregation. This is not the case in the allopatric areas. Hence the two species differentiate their microhabitat only when they are sympatric. The plant species associated mainly with the nest sites of *C. bicolor* indicate that this species prefers a type of vegetation that needs irrigation. This is in contrast to the nest sites of *C. savignyi*, which are usually found around plants that characterize typical dry steppe areas. As the ants' foraging paths recorded in the sympatric area reveal, *C. bicolor* performs significantly shorter foraging runs with respect to both length and time, and covers a much smaller foraging range than *C. savignyi* does. This result reflects the fact that the microhabitat occupied by the colonies of *C. bicolor* is richer in food abundance. When direct interspecific interactions were investigated by placing a bait midway between two heterospecific nests, *C. bicolor* foragers dominated over those of *C. savignyi*. The same dominance of *C. bicolor* over *C. savignyi* occurred in laboratory experiments. These results suggest that the dominant species drives the subordinate one out of the high quality microhabitats, and that the subordinate species is forced to survive in the less lucrative habitats. In conclusion, coexistence seems to be maintained by the asymmetric competitive relationship between the two species and the fact that the subordinate

species has the ability to endure in the less favourable microhabitat.

Keywords Competition · Interference · Interspecific interaction · Microhabitat · Sympatry

Introduction

Resource partitioning in one way or another is a necessary requirement, if competing species are to coexist sympatrically under resource-limited conditions (MacArthur 1972). This competition will be most severe between organisms that have similar demands. As related species tend to have similar ecological preferences, it has long been recognized that the phylogenetic relationships between species may influence their coexistence. Darwin (1859, p 76) wrote: "As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera." In a study on mammals Houle (1997) postulated that the intensity of behavioural competition among coexisting species is inversely proportional to their phylogenetic distance. This finding suggests that in order to understand the mechanisms of competing interactions and their impact on coexistence, competition should preferably be investigated among closely related species.

In ant communities, interspecific competition is a common phenomenon between cohabiting species (Wilson 1971; Brian 1983; Hölldobler and Wilson 1990). Many studies, which have investigated niche partitioning in ant communities, revealed that competition can result: (1) in direct antagonistic behaviour (Savolainen and Vepsäläinen 1988; Yamaguchi 1992; Retana and Cerdá 1995; Punttila et al. 1996; Cerdá and Retana 1998), (2) in temporal segregation (Baroni Urbani and Aktaş 1981; Marsh 1988; Fellers 1989; Deffernez et al. 1990; Cros et al. 1997; de Biseau et al. 1997; Cerdá et al. 1998; Retana

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and Cerdá 2000; Albrecht and Gotelli 2001; Campos and Schoereder 2001), (3) in spatial segregation by microhabitat differentiation (Punntila et al. 1996, Johnson 2000), or (4) in different foraging strategies (Traniello 1983, 1987; Jones and Sherman 1990; Perfecto 1994; de Biseau et al. 1997; Sanders and Gordon 2000).

In the present study, we examine niche separation and competition in the species pair *Cataglyphis bicolor* and *C. savignyi*. All *Cataglyphis* ants forage solitarily, never employing scent trails and never co-operating en masse. They occupy the particular niche of a thermophilic scavenger collecting the corpses of other arthropods that have fallen victim to the heat and desiccation stress of their harsh environment (Wehner et al. 1983, 1992; Cerdá et al. 1998). Hence they are “thermophilic” in the sense that they themselves must be active at the hottest time of day and year and must exhibit critical thermal maxima (CTM; values of about 52–53°C) that are higher than those of their prey species (Wehner et al. 1992; Gehring and Wehner 1995). As food densities are rather low in the arid habitats occupied by *Cataglyphis*, each individual must explore a large foraging area, within which it performs only a few foraging trips per day (Wehner et al. 1983; Schmid-Hempel 1983; Wehner 1987). The diurnal activity pattern has the additional advantage that during the foraging times of *Cataglyphis* potential competitors and predators reduce their activities by resting in the shade or hiding underground.

The phylogenetic proximity of the species pair *C. bicolor* and *C. savignyi* is well established. Molecular investigations have confirmed the conclusion drawn from recent morphological studies that the two species, even though they are morphologically nearly indistinguishable, form two separate, but closely linked phylogenetic lineages (sister species; Wehner et al. 1994; Dietrich and Wehner 1999). Within Tunisia the two species exhibit a parapatric pattern of geographical distribution (Fig. 1; Wehner et al. 1994). They have similar foraging behaviours and diets. As morphometric measurements show, head widths and tibia lengths — two characters successfully used in discriminating between *Cataglyphis* species (Wehner 1983) — do not differ between *C. bicolor* and *C. savignyi* (R. Wehner, unpublished data). Considering the phylogenetic proximity and the morphological similarity between these two sister species, it is reasonable to assume that within the area, in which the two members of this species pair coexist, competitive interactions should play a major role. To test this assumption, we recorded the spatial and temporal foraging patterns of *C. bicolor* and *C. savignyi* within the area, in which two species co-occur (the “sympatric area”) and in which heterospecific colonies could be found only a few metres apart. In addition, we determined the plant species present at the nest sites of the two *Cataglyphis* species first in the sympatric area and second in the allopatric areas of either species. The latter records should enable us to tell whether the two species shift their ecological preferences whenever they occur sympatrically.

Besides investigating this indirect (scramble) type of competition we tested whether the two species get engaged in direct (interference) types of interaction. In this context we performed aggression experiments in the laboratory as well as in the field. What we hoped to deduce from both kinds of analysis — on habitat partitioning and on direct interference — was an answer to the general question of how these two sister species of desert ants are able to coexist under nutritionally poor environmental conditions.

Materials and methods

Study sites

The majority of observations and experiments were carried out between 1996 and 1998 in the oasis El Guettar in central Tunisia (34°20'N, 8°55'E) (Fig. 1). At this study site the mean annual temperature is 19.7°C, and the driest months are July and August

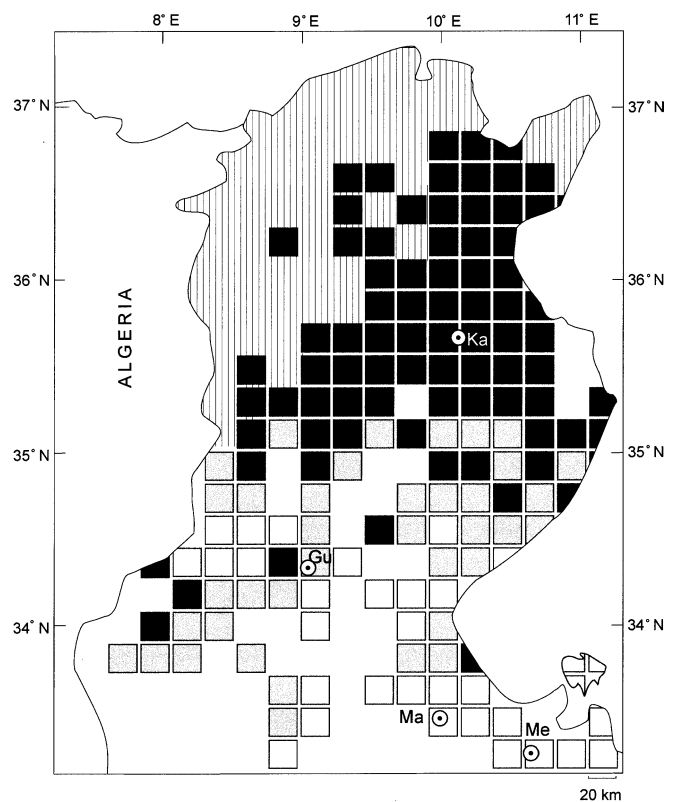


Fig. 1 Map of Tunisia exhibiting the distributional ranges of the sister species *Cataglyphis bicolor* and *C. savignyi*. Grey squares (20×20 km²) indicate the areas, where *C. bicolor* and *C. savignyi* occur sympatrically (central Tunisia). Regions containing allopatric populations of *C. bicolor* (central and northern Tunisia) and *C. savignyi* (southern Tunisia) are depicted by black and white squares, respectively. The hatched area marks the distributional range of *C. viaticus*, a third species belonging to the *bicolor* species group that occurs in the more mesic habitats of the Mediterranean zone of North Africa. White areas indicate that no sampling data are available (data and map based on Wehner et al. 1994). The study sites Kairouan (Ka), El Guettar (Gu), Matmata (Ma) and Medenine (Me) are marked by ⊙ signatures.

(national weather station, Gafsa). The barren natural steppe vegetation is dominated by *Artemisia herba alba* (Compositae), *A. campestris* (Compositae), *Diptotaxis harra* (Cruciferae), *Zygophyllum album* (Zygophyllaceae), and *Paganum harmala* (Zygophyllaceae). Small bushes of these plants cover about 30% of the ground. Within this natural steppe zone, olive trees are cultivated, and the El Guettar oasis comprises rich palm tree gardens. Two additional study sites were chosen for comparison: one in northern Tunisia next to the city of Kairouan, where *C. bicolor* is the only large *Cataglyphis* species, i.e. where it does not live sympatrically with *C. savignyi*, the other in southern Tunisia next to the towns of Medenine and Matmata, where *C. savignyi* occurs, but *C. bicolor* is lacking (Fig. 1). At the El Guettar ("sympatric") study site nine circular 785-m² areas (50-m radius) were selected within a 75-ha area, and within these circular areas the positions of all *C. bicolor* and *C. savignyi* nests were determined by means of a theodolite. In addition, in either allopatric area two such circles were laid out, and the *Cataglyphis* nest sites were recorded as described above.

Microhabitat segregation

Within a distance of 2 m from the nest entrance all plant species were determined using the botanical keys of Quezel et al. (1962–1963) and Ozenda (1991). In addition, plant species were verified by scientists at the Botanical Institute of the Faculty of Science of the University of Sfax.

The cover/abundance ratio of 73 plant species (according to the Braun-Blanquet index: Braun Blanquet 1932) and the percentage of the total fallow area were determined within a circular area (radius: 2 m) around the nest entrances of both *Cataglyphis* species. Thus for each of the 113 nest sites a wide set of variables was at hand, which was subsequently analysed with the software program MULVA-5 (Wildi and Orloci 1996).

A cluster recognition was performed to check for multivariate patterns in the vegetation types of each nest site: based on a resemblance matrix, which included the correlation coefficients of all the nest sites, a dendrogram was calculated using an agglomerative cluster analysis with complete linkage calculations (Wildi and Orloci 1996). This analysis reveals the grouping structure of the nest-site resemblances as visualized in a dendrogram. Later, an analysis of concentration showed whether the grouping or clustering was strongly related to a particular property of the data set, e.g. the type of ant species inhabiting a particular nest site. A distinct grouping structure with a good correlation to a certain factor is indicated by high deviations (Wildi and Orloci 1996). The first data set included nest sites from both the sympatric and the allopatric area ($n=113$), the second set contained the nest sites of only the sympatric area ($n=47$).

The discriminating power of single plant species can be measured by the F -values within a specific group classification (Wildi and Orloci 1996). The plant species can thus be ranked according to the decreasing order of their F -values [see Jancey's (1979) ranking of F -values]. The F -values for the plant species in the sympatric areas were calculated in order to determine the plants that are relevant for discriminating between the nest sites of *C. bicolor* and *C. savignyi*.

Daily activity patterns

At the El Guettar site the daily activity patterns of five heterospecific nest pairs of *C. bicolor* and *C. savignyi* (15–40 m apart) were recorded. For this purpose, all out-bound foragers (number of exits) of the focus nests were counted simultaneously on 5 days (1, 3, 6, 13, 16 May 1997). In addition, 20 foragers of each colony in the five heterospecific pairs were individually marked, in order to obtain an estimate of the number of daily foraging trips performed by individual ants.

Spatial foraging patterns

The spatio-temporal foraging patterns of individual ants were recorded in five different colony pairs, the members of which were located at inter-colony distances of 15–40 m. The paths of individual ants during their foraging trips were determined by following the ants and placing numbered labels on the ground at 1-min intervals. By determining the positions of the labels from a set of fixed reference points using a theodolite, the ants' foraging trajectories could be reconstructed. The foraging paths of the individual foragers were chosen randomly. A total of 99 foraging paths was obtained (54 paths in *C. bicolor*, 45 paths in *C. savignyi*). Foragers searching for solid food items (mainly dead arthropods) are called searchers. In contrast to the searchers, there are always some foragers that neither search for nor take in solid food items. Instead they lick secretions from plant surfaces. Based on the classification by Wehner et al. (1983), the foraging paths recorded were divided into paths of searchers and paths of lickers. The searchers' paths were further subdivided into two categories: successful searchers (ants returning to the nest with a food item) and unsuccessful searchers (ants returning with no food item). The records of search paths of lickers were aborted after the ants stayed at the same plant for >5 min (the intake of this type of food can last for >90 min). Since a few ants performed exceptionally long foraging paths, we used 10% trimmed means in order to calculate the average length, distances, and durations of the recorded paths. The duration, the total length, and the maximum distance from the nest entrance were analysed using the Mann-Whitney U -test at a significance level of $P<0.05$. However, for reasons mentioned above, the maximum distance from the nest entrance was the only parameter analysed in the lickers' search paths. In order to visualize the common foraging pattern of either species, a regression line was drawn through the interval points of the search paths of every ant. Then these regression lines were rotated such that they all fell together, i.e. all paths of one species were superimposed.

Direct interference

The direct interference between heterospecific foragers was investigated in an olive tree garden, which had been abandoned and had not been irrigated during the 2 preceding years. In this area several *C. bicolor* and *C. savignyi* nests were located only a few (3–4) metres apart. Artificial feeders were placed between two nests. All foragers arriving at the feeders were marked with a nest-specific colour, and the type of food carried back to the nest was recorded. The direct interspecific interactions at the baits were registered. The combats were judged to be won by a particular ant, if the ant had been able to prevent its opponent from getting to the food source and grasping a food item, or to be a tie, if either ant was able to grasp an item.

Confrontations between individual ants were also tested by placing single foragers of the two species into a test arena (floor area 15 cm×25 cm). During observation periods of 90 s (in two-thirds of the 126 tests) or 180 s (in one-third of the 126 tests) we determined which of the two colour-labelled individuals was superior or whether the confrontation ended in a tie. This final decision was based on the following types of behaviour (listed from low to high level of aggression): (1) mandibles in a threatening position, (2) biting of legs or antennae (3) dragging the competitor off after the superior animal had clenched its mandibles on the competitor's leg, and finally (4) injuring the competitor (for details see Dillier 1998). As a result of these aggressive behaviours the inferior animal usually retreated to a corner of the test arena. Three observers were involved in performing the test observations. After the 90-s or 180-s test periods the "human judges" always agreed which ant was superior, i.e. winner of the contest, or whether the contest had ended in a tie.

Results

Microhabitat segregation: comparison between allopatric and sympatric ranges of distribution

A botanical survey of the nest sites of *C. bicolor* and *C. savignyi* was performed in order to characterize the preferred microhabitats of the two *Cataglyphis* species. In total, >70 plant species were found around the 113 nest sites of both species within the sympatric and allopatric study areas (Fig. 1).

A first vegetation-type analysis included all nest sites within the sympatric and the two allopatric areas. The clustering pattern revealed four vegetation groups (Fig. 2), of which two were very species specific: groups 2 and 4 contained nearly exclusively nest sites that were inhabited either by *C. savignyi* or by *C. bicolor*, respectively. These species-specific vegetation groups were restricted to the sympatric nest sites. The *Cataglyphis* nest sites were less distinctly distributed among the other two vegetation groups (groups 1 and 3). These groups contained *C. savignyi* sites from the desert oases in southern Tunisia (allopatric sites) clustered together with some *C. bicolor* sites from the sympatric area and some nest sites from northern Tunisia (allopatric *C. bicolor* area). Furthermore, the microhabitat segregation was significantly more pronounced, if the sympatric nest sites were analysed alone (Fig. 3). Then two clear-cut species-specific clusters emerged: one group contained nearly all *C. savignyi* sites, the other all nest sites of *C. bicolor*. Only two *C. bicolor* sites clustered with the *C. savignyi* group.

As the analysis of concentration of the clustering patterns shows, there is a very strong species-specific microhabitat segregation of *C. bicolor* and *C. savignyi*, where the two species occur sympatrically (contingency coefficient, $C=0.85$). Such strong species-specific microhabitat preferences were not found in the set of nest sites including both the sympatric and the allopatric sites. In these areas C was substantially lower ($C=0.38$).

As to the key plant species characteristic for the *Cataglyphis* nest sites, *C. savignyi* sites were predominantly associated with *Artemisia herba alba*, *Arthrophytum scoparium* (= *Hammada scoparia*), and *Diploaxis harra* (indicated by the individual F -values as depicted in Table 1). These three species are typical for North African steppe zones, where they belong to the most dominant plant species (Frankenberg 1978; Quezel et al. 1962–1963; Ozenda 1991; Houerou 1969, 1995). They are even used to characterize the distinct features of the different steppe zones in North Africa (Houerou 1995).

On the other hand, *C. bicolor* nests were often associated with *Cynodon dactylon* (chien dent) and *Phoenix dactylifera* (date palm). Both plants are among the most commonly cultivated plants in Tunisian oases. Two other plants associated with *C. bicolor* nests are *Mesembryanthemum cristallium*, an indicator of rural zones with nitrogenous soil, and *Suaeda fruticosa*, a very halophilous plant (euhalophilous and mesohalophilous)

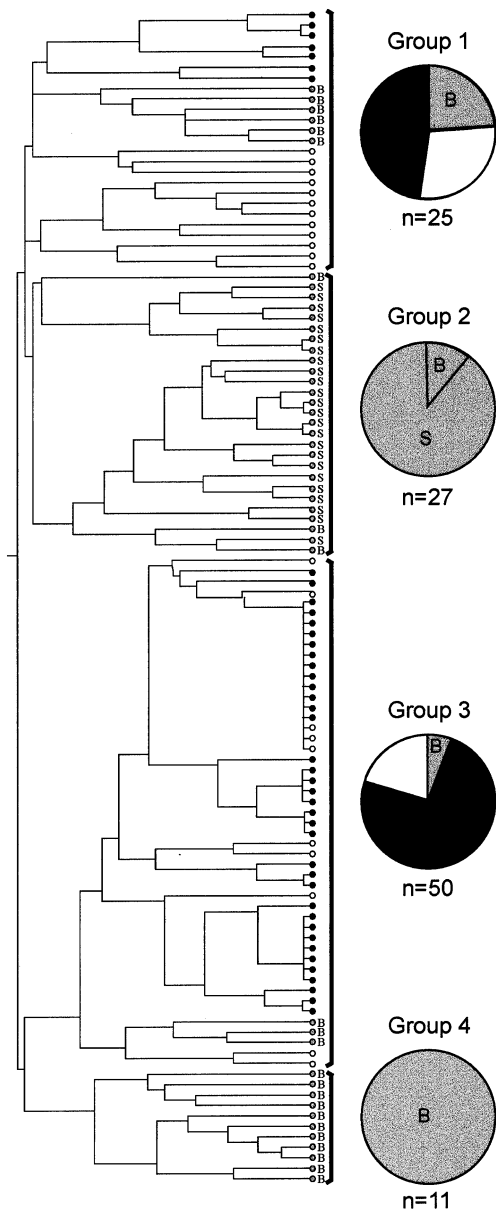


Fig. 2 Groupings of types of vegetation resulting from agglomerative cluster analyses of the vegetation at the ants' nest sites. In total 73 plant species recorded within a circular area (radius: 2 m) around the nest entrances of both *Cataglyphis* species were included in the analyses. The vegetation types fall into four large groups as indicated by the heavy black brackets to the right of the dendrogram. The circular diagrams represent the proportion of *Cataglyphis* species associated with the four main vegetation types. The pattern shown in this figure represents the analyses including all nest sites, i.e. the nest sites from the sympatric and allopatric distributional ranges of the two *Cataglyphis* species. Black (white) areas *C. bicolor* (*C. savignyi*) nest sites in the *bicolor* (*savignyi*) allopatric area, grey areas *C. bicolor* (B) and *C. savignyi* (S) nest sites in the *bicolor* and *savignyi* sympatric area, respectively, n number of nest sites within a particular group

also used as an indicator for irrigated areas (Houerou 1995; Quezel et al. 1962–1963).

In conclusion, *C. savignyi* nests are located in the natural steppe areas of southern Tunisia, whereas *C.*

Table 1 Ranking of the power (based on F -values) by which the occurrence of a particular plant species can discriminate between heterospecific nest sites. The F -values associated with the plant species indicate the plants relevant for the discrimination between

Rank	Plant species	F -value	<i>Cataglyphis</i> species
1	<i>Artemisia herba alba</i>	61.8	<i>C. savignyi</i>
2	Graminaceae	61.7	<i>C. savignyi</i>
3	<i>Cynodon dactylon</i>	46.5	<i>C. bicolor</i>
4	<i>Mesembryanthemum cristallium</i>	42.9	<i>C. bicolor</i>
5	<i>Suaeda fruticosa</i>	42.6	<i>C. bicolor</i>
6	<i>Phoenix dactylifera</i>	21.0	<i>C. bicolor</i>
7	<i>Arthropytum scoparium</i>	20.2	<i>C. savignyi</i>
8	<i>Diploptaxis harra</i>	13.7	<i>C. savignyi</i>

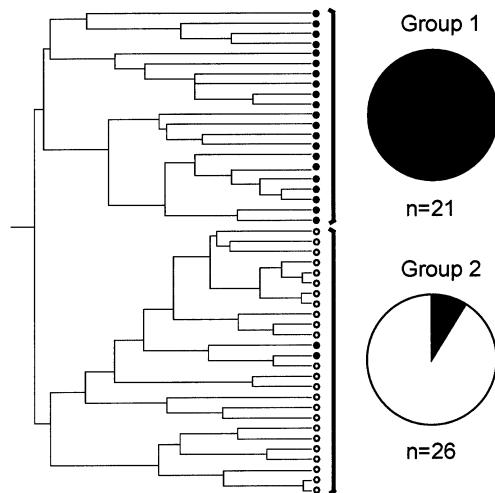


Fig. 3 Same as Fig. 2 but considers only the sympatric nest sites of *C. bicolor* and *C. savignyi*. For further information see Fig. 2. In particular, the black and white areas in the circular diagrams to the right represent the proportion of nests of *C. bicolor* and *C. savignyi*, respectively, within the two top-ranking types of vegetation

bicolor predominantly occupies the regularly irrigated spots in rural zones. In its allopatric area in central and northern Tunisia, in which annual rainfall is high enough (>200-mm) for wheat cultivation to be possible, the latter species inhabits the agricultural belt of Tunisia.

Plant species like *C. dactylon*, *Polygonum equisetiforme* or shoots of *Phoenix dactylifera* were associated with *C. bicolor* in the sympatric and in the allopatric area. In southern Tunisia — in the areas around Medenine and Matmata, which are climatically comparable to El Guettar — *C. savignyi* is allopatric. In this region *C. savignyi* nests were located next to the above-mentioned plants, which regularly need irrigation (Quezel et al. 1962–1963). These are exactly the microhabitats that within the sympatric zone are occupied by *C. bicolor*.

Spatio-temporal foraging patterns

As is the case in all *Cataglyphis* species, the two sister species considered here restricted their foraging activities

the nest sites of *Cataglyphis bicolor* and *C. savignyi* (as given in the last column) in the sympatric area: the higher the F -value, the better the discriminative power of a certain species of plant

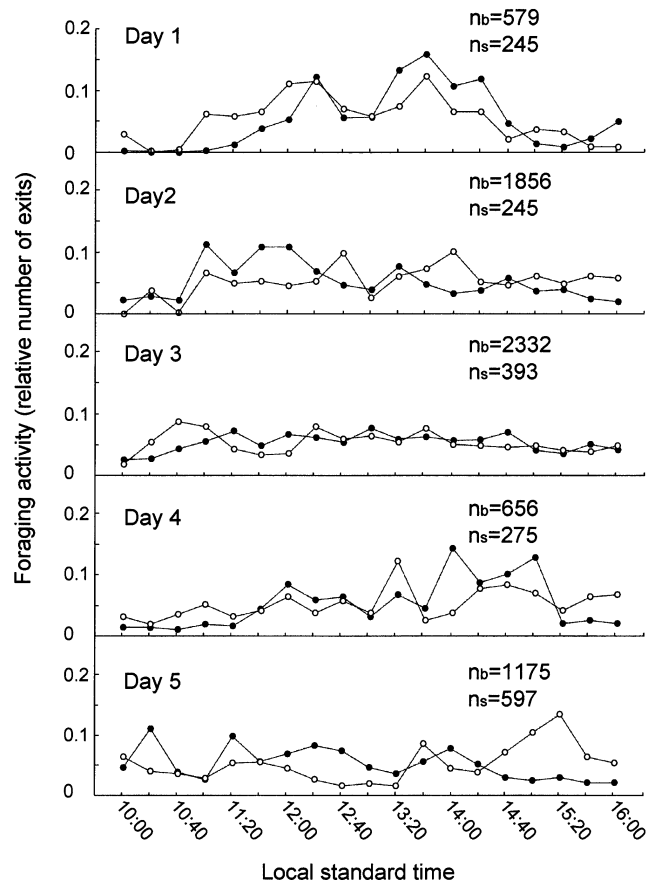


Fig. 4 Foraging activity patterns (exits of out-bound foragers) of *C. bicolor* (white) and *C. savignyi* (black) nests as recorded during a 5-day period. Activity is given as the ratio of the number of exits per 20-min interval and the total number of exits per 6-h observation period. *nb*, *ns* Numbers of foraging trips recorded per nest and observation period for *C. bicolor* and *C. savignyi*, respectively. Day 1 1 May, day 2 3 May, day 3 6 May, day 4 13 May, day 5 16 May

exclusively to day-time hours. The temporal profile of their activity patterns was very similar indeed (Fig. 4).

It did not reveal a pronounced daily activity peak at any particular time of day. It was affected mainly by the daily weather conditions. In general, clear skies increased activity, whereas cloudy skies decreased it. For example, on the first observation day the sky cleared at 1 p.m., and

Table 2 Comparison of foraging characteristics of individual ants of *C. bicolor* and *C. savignyi*. There are no significant intraspecific differences between successful and unsuccessful foragers in path

Characteristics of foragers	Path parameter	<i>C. bicolor</i> 10% Trimmed mean	<i>C. savignyi</i> 10% Trimmed mean	Mann-Whitney <i>U</i> -test <i>P</i> -value
Unsuccessful searchers	Length (m)	25.1	56.4	0.014
	Duration (min)	17.2	29.4	0.038
	Max. distance (m)	10.7	20.8	0.048
Successful searchers	Length (m)	22.1	57.2	0.023
	Duration (min)	7.6	22.7	0.004
	Max. distance (m)	10.1	26.2	0.005
Lickers	Max. distance (m)	11.1	22.0	0.016

length ($P=0.71$ and 0.85), duration ($P=0.09$ and 0.31) and maximal distance covered ($P=0.76$ and 0.24) for *C. bicolor* and *C. savignyi*, respectively

the activity of both species increased subsequently. On the second observation day the weather was rather cloudy. For the rest of the observation period it was sunny with little wind. As regards the behaviour of individual foragers the number of foraging trips performed per 6-h daily observation period did not differ between the two species (*C. bicolor* 3.5 ± 2.5 , $n=104$; *C. savignyi* 3.7 ± 2.4 , $n=91$; Mann-Whitney *U*-test, $P=0.30$).

In the sympatric areas the foraging ranges of the two species overlapped widely. While covering the same foraging grounds, *C. bicolor* and *C. savignyi* exhibited very similar foraging strategies. A forager would run either straight to a known food source (e.g. to lick secretions of plant surfaces), or search randomly for a solid food item. Having found and grabbed a food item, the successful forager would carry it immediately back to the nest along a straight inbound path. However, the two species differed in their foraging ranges: the journeys of *C. bicolor* were shorter than those of *C. savignyi*. This applies to unsuccessful and successful foragers as well as to scavengers and plant lickers. It relates to the length and duration of a foraging trip as well as to the maximal foraging distance from the nest. The differences are significant at least at the 0.05 level, in some cases also at the 0.01 level (Table 2).

Figure 5 shows that, for example, 90% of the foraging activity of unsuccessful searchers of *C. bicolor* occurred within a distance of 14.5 m from the nest entrance, whereas the unsuccessful foragers of *C. savignyi* exhibited 90% of their foraging activity within a distance of 21 m. Furthermore, *C. bicolor* and *C. savignyi* searched for the same type of food (plant liquids and solid food items) in similar proportions, and both species were equally successful (Table 3). The items they collected depended mainly on the resources available. In addition, the temperatures measured immediately after the completion of a foraging round trip did not differ significantly between the two species. Measurements were taken 1 cm above the ground in the shade (*C. bicolor*, 34.0°C , $n=54$; *C. savignyi*, 32.9°C , $n=45$; Mann-Whitney *U*-test, $P=0.23$). Furthermore, the CTM values of the two species lie between 52°C and 53°C and are not significantly different from each other (R. Wehner, unpublished data).

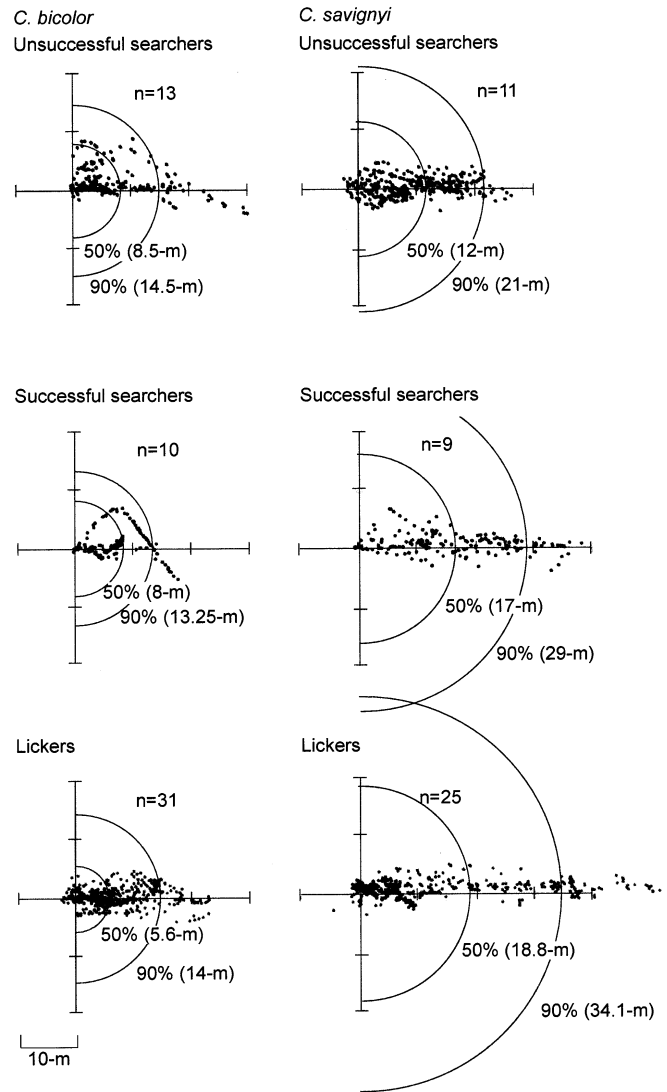


Fig. 5 Foraging ranges of *C. bicolor* and *C. savignyi*. The centres of the orthogonal axes mark the location of the nest entrances. Dots indicate the ant's locations recorded in 1-min intervals. The semicircular lines denote the distances within which 50% and 90% of all 1-min points are located. *n* Number of foraging paths per plot

Table 3 Search path categories of *C. bicolor* and *C. savignyi* within the sympatric distributional range of the two species. The data were taken during the spring season (6–29 April) on 15 different days at five different pairs of heterospecific colonies located at the El Guettar study site

	<i>C. bicolor</i>		<i>C. savignyi</i>	
	Number of runs	%	Number of runs	%
Unsuccessful searchers	13	24.1%	11	24.4%
Successful searchers	10	18.6%	9	20.0%
Lickers	31	57.4%	25	55.6%
Total	54	100%	45	100%

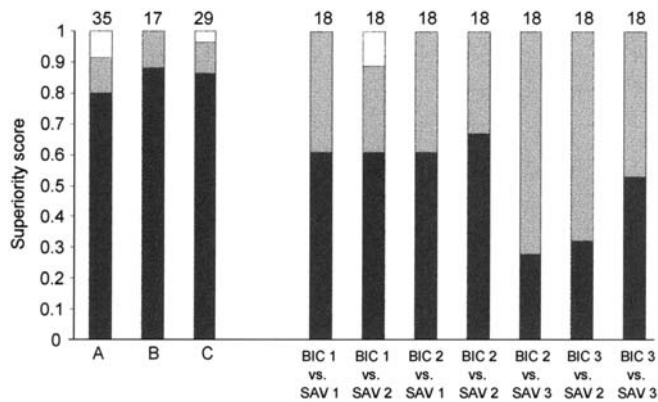


Fig. 6 Direct heterospecific interactions of workers of *C. bicolor* and *C. savignyi*. In each interaction the superior individual was scored (black area *C. bicolor* was superior, white area *C. savignyi* was superior, grey area interactions ended in a tie). Numbers above the bars indicate the number of encounters recorded. *Left-hand histogram* Interactions recorded at artificial bait stations in the field. A–C Results of tests performed on 27, 28, and 29, April, respectively. *Right-hand histogram* Interactions recorded within laboratory test arenas. Individual ants of three different colonies of both species [*C. bicolor* (BIC), BIC 1, BIC 2, BIC 3 and *C. savignyi* (SAV), SAV 1, SAV 2, SAV 3] were tested in pairwise encounters

Direct interference

Whenever foragers of the two species arrived simultaneously at a feeding station, short aggressive interactions were observed. Usually these fights ended after a few seconds with the withdrawal of one or both ants from the bait. Often several simple threats with the mandibles scared the opponent ant away from the food bait. The subordinate ants showed a typical “flee and return” strategy, i.e. fleeing over a distance of about 60 cm and returning to the source thereafter (as described for other formicine ants by Mercier and Dejan 1996). The left-hand part of Fig. 6 shows that the workers of *C. bicolor* were more often able to repel their opponents in the heterospecific fights than workers of *C. savignyi* were.

The dominance of *C. bicolor* could be demonstrated in laboratory experiments as well. In these tests the heterospecific ants taken from their colonies were forced to interact by a simple experimental design: the two combatants encountered each other within a small perspex chamber in which the escape distance was limited. In 126 encounters recorded in seven pair-wise groupings of members of three *C. savignyi* and three *C. bicolor* colonies (Fig. 6, right-hand part) *C. bicolor* was success-

ful in rejecting its heterospecific opponent much more often (52% of the total number of encounters) than *C. savignyi* was (only 2% of cases). However, almost half of the encounters (the remaining 46%) ended in a tie: after a brief encounter accompanied by threats with the mandibles, both ants retreated and usually rested for a few seconds in a corner of the arena.

Discussion

The present investigation focuses on the coexistence of the two parapatric sibling species of desert ants, *Cataglyphis bicolor* and *C. savignyi* (*bicolor* species group). Due to their morphological similarity these two species — together with a third species, *C. viaticus* — have long been described as one species (*C. bicolor*; Santschi 1929). More recent investigations of various morphological characters including male genitalia and worker pubescence as well as molecular analyses clearly show that *C. bicolor* and *C. savignyi* actually form two separate species (Dietrich and Wehner 1999; Wehner et al. 1994). In southern Tunisia these two almost morphologically identical species coexist (sympatric area). Thus, the two sibling species provide an excellent system with which to examine resource partitioning in competing species.

Based on a microhabitat vegetation-type analysis, in their sympatric area *C. bicolor* and *C. savignyi* exhibit clear-cut nest site specializations, although the colonies of the two species can sometimes be found only a few metres apart, and their foraging ranges can overlap extensively (see also Dillier 1998 for a study site near Maharès, 150 km north-northeast of the El Guettar study site). In the sympatric area the *C. bicolor* nest sites are usually located next to *Cynodon dactylon* and *Phoenix dactylifera*, which are among the most commonly cultivated and hence regularly irrigated plants in Tunisian oases. By providing rich food resources these two plant species are indicative of a microhabitat containing more biomass than is the case for non-irrigated spots within the same geographical zone. In contrast, the sympatric nest sites of *C. savignyi* are found in the vicinity of typical dry steppe plants (e.g. *Artemisia herba alba*, *Arthrophytum scoparium*, and *Diplotaxis harra*).

In the allopatric area, however, we did not find any species-specific type of segregation. In its allopatric region *C. savignyi* is often associated with plants characteristic for *C. bicolor* in the sympatric area (e.g.

Cynodon dactylon, *Phoenix dactylifera*). Obviously, where *C. savignyi* occurs alone, it prefers the very microhabitats that are occupied by *C. bicolor* in the sympatric area.

In addition, the present study revealed subtle differences in the foraging characteristics of the two species. In the sympatric area *C. bicolor* performed significantly shorter foraging trips than *C. savignyi* did (in terms of length, duration, and maximal distance from the nest entrance; Table 2), even though both species employ similar spatial and temporal foraging strategies and subsist on the same type of food. The result that *C. bicolor* performs shorter round-trips and, thus, forages more efficiently than *C. savignyi* does, is most likely due to the richer food abundances in the microhabitats around its nest sites rather than to intrinsic behavioural differences between the two species. The immediate surroundings of the nests of *C. bicolor* provide rich hunting grounds, whereas *C. savignyi* foragers are forced to run further and have to search longer in order to be successful.

We can only agree with what Bernstein and Gobbel (1979) state in their study about partitioning of space in ant communities: "Perhaps the most important factor contributing to the success of an ant colony is where it is located."

A species can tolerate a certain range of physical factors — temperature, humidity, radiation, etc. — and can theoretically be found wherever these tolerance limits are satisfied (Ridley 1996). This area is termed the fundamental niche of the species. However, the theoretically possible distribution may be limited by competition with coexisting species (realized niche). Microhabitat differentiation between coexisting species can be caused, for instance, by aggression of the dominant species. Then, the dominant species forces the subordinate one to reduce its realized niche.

One of the rare studies, in which closely related coexisting ant species have been investigated, is that by Greenslade (1974) on two parapatric forms of the Australian meat ant *Iridomyrmex purpureus*. One form occupies the lower, the other the higher rainfall zones of the study area. The two forms of *Iridomyrmex* ants meet along a boundary area, where a clear microhabitat segregation occurs. Using descriptive methods, by analysing the spatial distribution of the colonies of the two forms, Greenslade (1974) showed that in the sympatric area one form appears to be dominant and capable of displacing the other one. However, only once did Greenslade observe a direct interference interaction between heterospecific individuals.

Does such interference competition occur in *Cataglyphis*, and does it complement the dominance by scramble competition of *C. bicolor* that we have established by analysing the microhabitat preferences and foraging characteristics of the two species? Both our field and laboratory experiments answer these questions in the affirmative. For example, in the field *C. bicolor* was highly dominant in driving off *C. savignyi* from a jointly visited bait, but never rejected its heterospecific competi-

tor completely from the food source. These results suggest that in spite of the dominance of *C. bicolor*, *C. savignyi* has the ability to survive in the sympatric area by shifting its nest sites to a different type of microhabitat. Hence, the fundamental niche of *C. savignyi* is large enough to cope with suboptimal conditions. Using an "avoidance tactic" *C. savignyi* shifts its realized niche into the dryer steppe microhabitats. The fact that in the allopatric region — i.e. in the absence of competition with *C. bicolor* — *C. savignyi* prefers nest sites situated next to irrigated plants, supports the hypothesis that in the sympatric region the two species compete for the same microhabitats.

Were it not for this kind of direct interference between the two species one could suggest the possibility that any difference observed between sympatric and allopatric populations reflects interspecific geographic variation as a result of adaptation to local environmental conditions rather than a response to the presence or absence of heterospecific ants. First, our observations and experiments which investigated direct interference do not support this possibility. Secondly, and more directly, our work in progress on the molecular systematics of *Cataglyphis* species shows that the very same species-specific haplotypes occur in both *C. bicolor* and *C. savignyi*, throughout the entire geographical range of this study.

Another way of obtaining indirect experimental evidence for competition in the field, and hence addressing the former question, could be achieved by removal experiments (Schoener 1974; Perfecto 1994; Cerdá and Retana 1998). By removing the dominant species and thus eliminating competition one can directly observe the subordinate species' behaviour. If competition between the two species played an important role, the subordinate species should take over the microhabitat of the dominant species. Cerdá and Retana (1998) included removal experiments in their study of interference interaction between two sympatric ant species that had been found to abandon their nests as a consequence of attack encounters. The authors concluded from their removal experiments that competition for nest sites was more likely to occur than competition for food resources.

Of course, due to their long generation times, social insects are not ideal candidates for such removal experiments (Schoener 1974; Schmid-Hempel 1983). It would take several months or even years to obtain reliable results, especially if one worked with ant species such as *C. bicolor* or *C. savignyi*, whose colonies are widely spaced and whose foraging area cover thousands of square metres. Furthermore, *C. bicolor* and *C. savignyi* are polydomous species (see also Dillier 1998). In order to dislocate an entire colony, one has to locate and remove all nests belonging to such a colony. As this is an extremely difficult endeavour, we refrained from performing such experiments.

Sanders and Gordon (2000) used another approach to examine how interspecific competition between *Myrmecystus* species and *Aphaenogaster cockerelli* affects the

resource use and behaviour of either species. They placed temporary enclosures around *Myrmecystus* spp. colonies and recorded the resources collected by *A. cockerelli*. When neighbours were enclosed, *A. cockerelli* colonies collected significantly higher proportions of termites and less plant matter than when neighbours were active. The number of ants engaged in foraging behaviour and nest maintenance work increased as well. Thus this experimental study shows that interspecific interactions can affect the behaviour and resource use of competing ant colonies. It would be interesting to enclose *C. bicolor* nests in order to see if *C. savignyi* foragers do increase their foraging activity correspondingly. However, the foraging ranges of *Cataglyphis* desert ants are rather large, and food in the North African arid zones is widely spread. Hence, the effect of enclosing competing *C. bicolor* colonies for a few days might not have as pronounced an effect for the subordinate *C. savignyi* as enclosing *Myrmecystus* colonies had for the subordinate *A. cockerelli*. It is more likely that *C. bicolor* dominates *C. savignyi* when young colonies are establishing themselves.

In conclusion, in central Tunisia the two parapatric sibling species *C. bicolor* and *C. savignyi* partially overlap in their distributional ranges. Within this "sympatric area" they exhibit clear-cut microhabitat specializations. *C. bicolor* inhabits the nutritionally richer microhabitats and thus can afford to perform shorter foraging runs. Furthermore in direct interactions *C. bicolor* significantly dominates *C. savignyi*. Obviously, the dominant *C. bicolor* species drives the subordinate *C. savignyi* out of the better quality microhabitats, but the subordinate species can survive in the less rich habitats. Based on the extensive analysis of the type of vegetation associated with the nesting sites of the two species in their sympatric and allopatric areas we conclude that it is mainly differential microhabitat selection that enables the coexistence of the two sibling species.

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