

Research article

Spatio-temporal patterns of colony distribution in monodomous and polydomous species of North African desert ants, genus *Cataglyphis*

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Summary. Two monogynous species of North African desert ants belonging to the formicine genus *Cataglyphis* exhibit extremely different habitat preferences, population densities, and population structures. *C. fortis* is the only *Cataglyphis* species within the salt-pan flats of the Algerian and Tunisian chotts and sebkhas, whereas *C. bicolor*, alongside *C. albicans* and *C. ruber*, inhabits the nutritionally richer low-shrub semi-deserts surrounding the salt pans. We present a comparative study of the spatio-temporal patterns of colony distribution of the two monogynous species over periods of at least 5 (maximally 15) years. In *C. fortis* low population densities (0.5 kg body mass per km²) and, correspondingly, large inter-nest distances (40.6 m mean nearest neighbour nest distance) are correlated with absolute intra-annual and high inter-annual nest-site stability (more than 75% inter-annual survival rate) and a monodomous colony structure. In *C. bicolor* the population density is one hundred times higher (42 kg body mass per km², 9.1 m mean nearest neighbour nest distance), nest-site stability is extremely low in both intra-annual and inter-annual terms (67% intra-annual survival rate for 13-day periods; less than 5% inter-annual survival rate), and polydomy prevails. These marked differences in population structure are discussed with respect to adapted traits such as foraging range, running speed, and relative lengths of the legs.

Key words: Ants, *Cataglyphis*, nest distribution, nest relocation, monodomy, polydomy.

Introduction

Competition is the hallmark of interactions among ant colonies. Whatever the behavioural traits may be that have

ultimately evolved as a consequence of competitive interactions between members of different colonies, the final outcome of these behaviours reflects itself in the distributional pattern of its colonies in space.

In the present account we investigate the population structure of two species of desert ants *par excellence*, i. e., of ants belonging to the Old World genus *Cataglyphis*. One of the two species, *C. fortis*, inhabits the most food-impooverished areas of the North African deserts, the salt pans of Tunisia and northern Algeria. If we move into the centres of these salt flats, *C. fortis* is the only *Cataglyphis* species, actually the only ant species at all. Hence the question arises whether the spacing of the colonies of this North African salt-pan endemic follows the general overdispersion pattern known for ants (see, e. g., Levings and Traniello, 1981; Levings and Franks, 1982; Hölldobler and Wilson, 1990), or whether the extreme shortage of food in the habitat of this species has led to other distributional patterns.

The second species, *Cataglyphis bicolor*, inhabits the nutritionally richer low-shrub desert surrounding the salt pans. How, then, does population structure of this species compare with that of *C. fortis*? This is an intriguing question all the more as *C. bicolor* and *C. fortis* share their major foraging characteristics such as type of food (arthropod carcasses), time of foraging (exclusively at daytime and in the summer season), or search strategy (sector fidelity even under conditions of uniformly distributed food resources). We try to answer this question not only by static surveys of colony distribution patterns but also by monitoring temporal changes of these patterns within the same test areas over periods of several years. The differences found between the two species can be correlated with species-specific morphological and behavioural characteristics such as body size, running speed (Wehner, 1983), and foraging range (Wehner, 1987), with the occurrence of monodomous or polydomous colony structures, and finally with the presence or absence of multi-congeneric-species associations (Wehner et al., 1983; Schmid-Hempel, 1984).

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Materials and methods

1. Ant species

The current study focuses on two monogynous species of the formicine genus *Cataglyphis* (Foerster, 1850; Wehner, 1983; Agosti, 1990; Wehner et al., 1994). In Tunisia the large reddish-black polydomous *Cataglyphis bicolor* (Fabricius, 1793) inhabits the steppe areas of the Tunisian Sahel (Wehner et al., 1994; Dietrich and Wehner, 2003) as well as agricultural areas, pasturelands and settlements. The medium-sized monodomous *Cataglyphis fortis* (Forel, 1902; Wehner, 1983) is restricted to the relatively wet and salty soils of the chotts, sebkhas and offshore inundation areas. The North African zone of the chotts extends from southern Tunisia to the North-east of Algeria. *C. fortis* is endemic to this area.

The *C. bicolor* study site is inhabited also by two small *Cataglyphis* species, *C. albicans* (Roger, 1859) and *C. ruber* (Forel, 1903; Wehner, 1986), which are included in certain parts of this study. In Tunisia *C. ruber* occurs south of a line combining Biskra, Feriana and Sfax, i.e. south of approximately 35°N latitude. *C. albicans* is perhaps the most widely distributed *Cataglyphis* species in Tunisia. Its distributional range overlaps with *C. bicolor* and *C. ruber* as well as with *C. viaticus* in the north and *C. savignyi* in the south of the *bicolor* study site. It extends even into the fringes of the *fortis* study site, where the ground is sparsely covered with islands of low-shrub vegetation.

2. Field study sites

Most field data were collected during the 5-year period of 1987–1991 at our study site near Maharrès (34.58°N, 10.50°E), Tunisia, about 30 km south of Sfax. Partial recordings were continued until the year 2002.

The *fortis* study site is located within a salty coastal plain characterized by large barren surfaces. The soil consists of a mixture of sandy clay and gypsum. Occasionally inundated during the winter months, the surface dries slowly during March and April. Due to high evaporation rates, a hard, smooth, brownish-yellow surface develops. Towards the sea this hard, solid ground is replaced by a salt-swamp tidal seashore environment covered patchily by halophilous chenopodiacean shrubs (mostly *Arthrocnemum glaucum*). On the inland side the bare surface of the *fortis* study site blends with the shrub desert of the *bicolor* study site (see below).

The *C. fortis* nest sites are located in open, vegetation-free areas of the salt-pan habitat. The nest entrances can be found on top of hardly detectable elevations of the ground, but never in, or close to, patches of the sparse vegetation.

The *bicolor* study site is located within the shrub desert characteristic for the pre-Saharan zone of the Tunisian Sahel (150–200 mm rainfall; Le Houerou, 1969; Floret et al., 1982). The sandy clay soil surfaces often forming thin lime and gypsum crusts are patchily covered with chenopodiacean shrubs such as *Suaeda vermiculata* and *Salsola longifolia*, but also with *Arthrocnemum macrostachyum* and *Atriplex* species as well as with the thorny zygothylacean bushes of *Nitraria retusa*. These visually dominant shrubs and bushes are interspersed with a mosaic of low xerophyllous dwarf shrubs, grass horsts (*Lygeum spartum*, *Cynodon dactylon*) and low grasses (*Koeleria pubescens*) as well as with patches of perennial herbs (e.g. the cariophyllacean *Minuartia geniculata*, the cistacean *Helianthemum lippii*, or the scophulariacean *Kickxia aegyptiaca*) and some inconspicuous (mostly asteracean) annuals (for a complete plant list of the study site see Neumeyer, 1994). The *bicolor* study site extends between the sea and patchily distributed *fortis* habitats on the one side and agricultural lands (olive tree cultures) on the other.

The *C. bicolor* nest sites can be found within patches of vegetation as well as on the bare ground in between. Even though there does not seem to exist any correlation between the distribution of nests and large-scale features of the habitat, mechanical disturbances of the hard steppic ground such as, e.g., rodent holes seem to favour the initiation of new nests and hence influence the small scale location of the nest entrances.

3. Spatial distribution of nests and colonies

Nest sites were first localized by systematic searches, i.e. by patrolling the test area along parallel lines 5 to 10 m apart (depending on vegetation density), searching for new nest sites, and checking all former (labelled) nest sites. The search was supported by feeding biscuit crumbs to foragers in the field and subsequently pursuing the biscuit-carrying workers back to the entrances of their nests. The locations of the nests were then mapped to the nearest five centimetres by using a theodolite with infrared distancer (Leica Geosystems AG, CH-9435 Heerbrugg) or by applying a right-angle measurement method employing an optical square consisting of two superimposed pentagonal prisms (Leica Geosystems AG), and three alignment rods as well as a 50-m tape-measure (a standard technique in geodesy). These mappings occurred 3 to 6 times during the ants' annual activity season from March to October over periods of at least four and maximally nine successive years.

In *C. bicolor* and *C. fortis* these exhaustive mappings of nest entrances occurred in focus areas of $3.5 \cdot 10^4$ m² and $1.0 \cdot 10^5$ m², respectively. In order to account for edge effects, nests were mapped also outside these focus areas. During the sampling periods the states of activity of the nests were recorded. In the polydomous species *C. bicolor* special care was taken to monitor all 'carrier transports', i.e. above-ground transports of brood or nest mates by experienced foragers between different nests belonging to the same colony (Wehner et al., 1972). Following transporter ants enabled us to determine the colony affiliations of satellite nests. Source and target nests as well as the transported load (eggs, larvae, pupae, workers or sexuals) were noted.

The digitized coordinates of the mapped nest entrances were statistically and graphically evaluated by employing the SAS software package (SAS of Institutes Inc., Cary, NC, USA). In order to evaluate the spatial distributions of nests and colonies we performed the nearest neighbour distance analysis as described by Clark and Evans (1954). This 'plot-less' or continuous method was preferred to discrete methods based on a Poisson distribution of points within a raster of plots (Harkness and Isham, 1983; see also Greenslade and Halliday, 1983; Johnson, 1992). As the nearest neighbour distance analysis is not very sensible to the absolute nest (or colony) density as well as to the frequency of data acquisition, it allows for comparisons between locally and temporally separated sets of data. In order to avoid edge effects, nests lying outside the test area were frequently included, and the modified formula provided by Donnelly (1978) was used (Sinclair, 1985; Haefner et al., 1991; Franks and Sendova-Franks, 1992; Ryti and Case, 1992). As the uncorrected Clark and Evans (1954) formula tends to be biased, especially for small values of N, towards a regular distribution (Donnelly, 1978; Sinclair, 1985), we always used the corrected version (see also Dale et al., 2002; Perry et al., 2002).

Statistical differences between nest and colony distribution patterns were examined by performing an ANOVA for differences between test periods, test areas (Clark and Evans, 1954), and species effects (orthogonal linear contrasts: Linder and Berchtold, 1979; Sachs, 1992). A cluster analysis (Proc Cluster, centroid cluster analysis, SAS Institute Inc., Cary, NC, USA) helped to infer the colony affiliations of *C. bicolor* nests from the geometric nest distribution pattern, minimizing the distance of the member nests to the geometric centre of the cluster. The resulting clusters were checked for inconsistencies with colony affiliations determined from the 'carrier transport' data. The iteration process of the cluster analysis was stopped at the cluster number with the least contradictions to the 'carrier' data. All ambiguities in colony affiliation have been resolved in favour of the 'carrier transport' data.

Results

1. Population densities and patterns of distribution

A comparison of the nest-site distributions of *C. fortis* and *C. bicolor* (Figs. 1 A and B, respectively) reveals the obvious: the density of nests is much higher – by a factor of about five

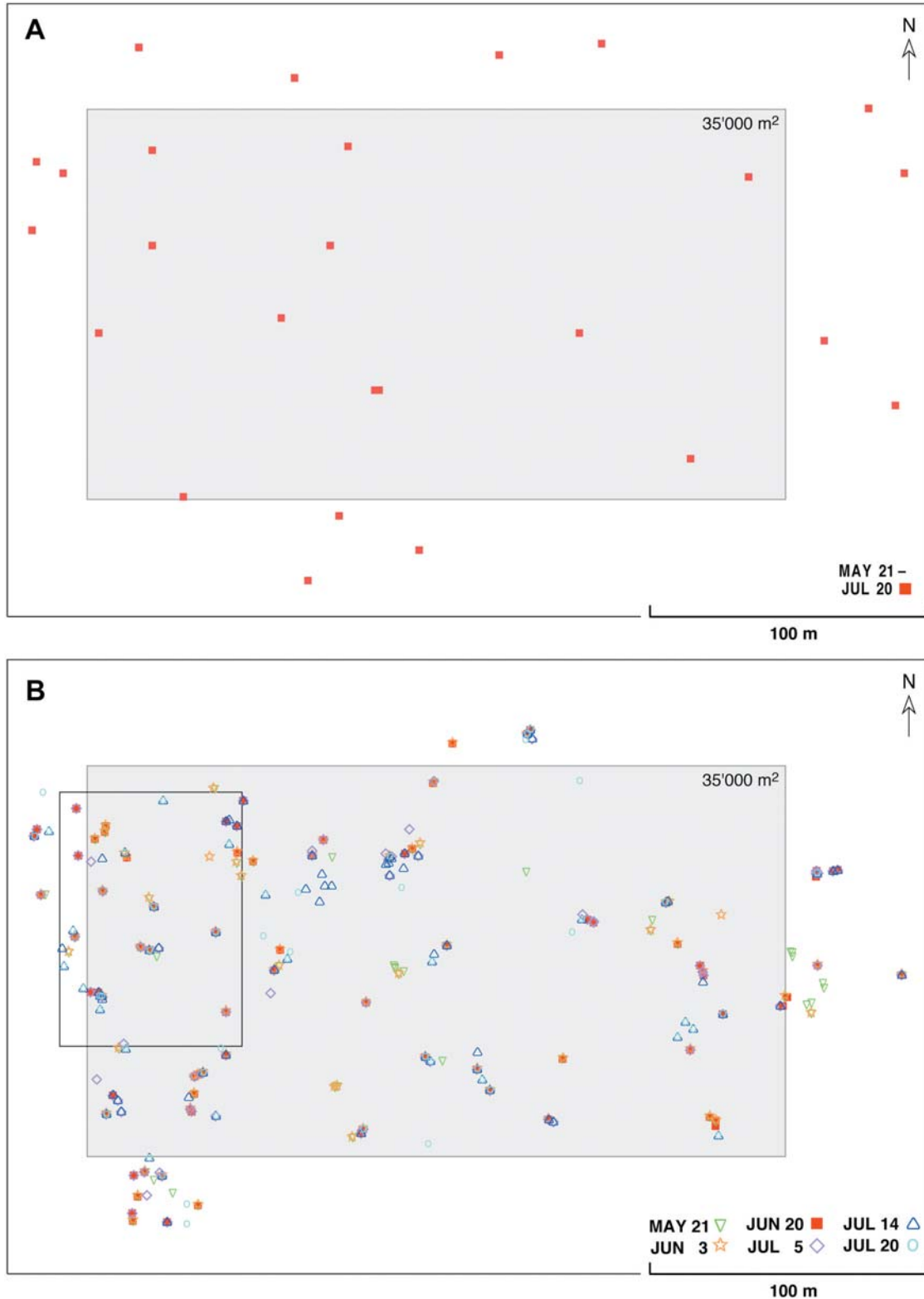


Figure 1. Nest site maps of **A** *C. fortis* and **B** *C. bicolor* in 1989: intra-annual variation. In *C. fortis* the nest sites remained constant throughout the entire summer activity period of the species, but this was not the case in *C. bicolor*. The different symbols represent nest localities recorded at six different times of the ants' peak activity period, May–July. The localities recorded on June 20 (filled symbols) provided the data set used in the inter-annual comparison (Fig. 4). At the *fortis* study site (A; test area for experiments on ant navigation, Wehner, 2003) nests were recorded routinely many times during the period May 21 to July 20. Open symbols, nest entrances active before or after the focus period. The insert frame in **B** marks the location of the more detailed map in Fig. 2

Table 1. Nest site distribution patterns of all mapped nests in the “fortis study site”. The table shows the Nearest-Neighbour-Analysis for the mapped *C. fortis* nest entrances for summer 1988 to 1991. The table includes the numbers of nests, the sizes of the mapped area, the nest densities, r mean values and $\pm sr$ standard errors of the nearest neighbour nest distances, r_{th} theoretical mean value and $\pm \sigma r_{th}$ standard error of the expected nearest neighbour nest distances in an infinitely large random distribution for the observed nest densities, the ratio $R = r/r_{th}$ as a measure of the degree to which the observed distributions depart from random expectation (0 = maximal aggregation, 1 = random distribution, 2.15 = regular distribution/maximal spacing), and $c = (r - r_{th})/\sigma r_{th}$ the standard variate of the normal curve (one-sided test). In 1988 a larger area has been sampled

Year	N	Area [m ²]	Density [10 ⁻⁴ m ⁻²]	$r \pm sr$ [m]	$r_{th} \pm \sigma r_{th}$ [m]	R	c	P
1988	38	14 · 10 ⁴	2.71	41.86 ± 16.54	33.20 ± 3.12	1.26	2.78	0.003
1989	35	10 · 10 ⁴	3.50	37.65 ± 11.14	29.88 ± 2.96	1.26	2.62	0.004
1990	32	10 · 10 ⁴	3.20	39.05 ± 12.53	31.42 ± 3.27	1.24	2.33	0.010
1991	26	10 · 10 ⁴	2.60	44.45 ± 16.66	35.33 ± 4.10	1.26	2.22	0.013

Table 2. Nest site distribution patterns at the “bicolor study site”. The table presents the Nearest-Neighbour-Analysis for the *C. bicolor* nest entrances, which have been active in June–July during the summers of 1988 to 1991 (see marked area in Fig. 4B). For definitions and conventions see Table 1

Year	N	Area [m ²]	Density [10 ⁻⁴ m ⁻²]	$r \pm sr$ [m]	$r_{th} \pm \sigma r_{th}$ [m]	R	c	P
1988	39	3.5 · 10 ⁴	11.14	9.75 ± 10.54	16.13 ± 1.48	0.60	-7.46	<0.001
1989	57	3.5 · 10 ⁴	16.28	8.66 ± 8.63	13.16 ± 0.99	0.66	-8.75	<0.001
1990	42	3.5 · 10 ⁴	12.00	10.00 ± 12.01	15.49 ± 1.36	0.65	-4.36	<0.001
1991	77	3.5 · 10 ⁴	22.00	8.47 ± 6.15	11.22 ± 0.72	0.75	-3.83	<0.001

– in *C. bicolor* than it is in *C. fortis*. As can be deduced from the data presented in Tables 1 and 2, the densities amount to 300 ± 42 nests per km² in *C. fortis* and $1'535 \pm 497$ nests per km² in *C. bicolor* (mean \pm standard deviation, N = 4 years). This difference is in accord with the extremely poor nutritional value of the *C. fortis* habitat, the salt-pan flats, as compared to the low-shrub semi-desert inhabited by *C. bicolor*. Furthermore, during the ants' (summer) activity period the nest sites of *C. fortis* are extremely stable, but the ones of *C. bicolor* shift around substantially. In Fig. 1B the filled red squares depict nests active during the peak of the annual activity period, the end of June, whereas the open symbols represent active nests recorded before and after that peak period. During 6 sampling periods separated by 12.6 ± 6.4 days within a 3-month period (May–July) Nest Renewal and Nest Remaining Indices (Cerdea et al., 2002) were $30.1 \pm 6.8\%$ and $66.7 \pm 12.3\%$, respectively. The functional correlate underlying this pronounced spatial shifting of nest sites in *C. bicolor* will become apparent later.

First, let us ask whether the marked difference between the population densities of the two *Cataglyphis* species is correlated with corresponding inter-species differences in the kind of pattern, in which the nest-sites are spatially distributed. To answer this question we used the measure of spacing first proposed by Clark and Evans (1954) and based on the criterion of nearest neighbour distances (see Methods). In particular, we determined the mean nearest neighbour distances of the nests, r , and compared these values with the theoretical mean distances to the nearest neighbours that would be expected if the nests were distributed randomly, r_{th} . By definition, in the latter (random) case the ratio of the val-

ues r and r_{th} is $R = r/r_{th} = 1$. However, as shown by the R-values in Tables 1 and 2, the nest-site distributional patterns of the two species depart highly significantly from randomness, but do so in different directions. In *C. fortis* the ratio $R = 1.26 \pm 0.01$ deviates significantly from $R = 1$ towards $R = 2.15$, that is, towards the value representative for maximum spacing, in which all nests are distributed in an even, hexagonal way (uniform distribution, overdispersion). Note that all *C. fortis* data mentioned above and given in Table 1 are derived from nest-site records that have been taken within an area about three times as large as the focal area shown in Fig. 1.

In contrast to *C. fortis*, the R-value of the nest-site distribution of *C. bicolor* is significantly smaller than one ($R = 0.67 \pm 0.06$; Table 2) indicating a clear tendency towards an aggregated (under-dispersed) distribution. Even a cursory glance at the inner (focal) area of the *C. bicolor* nest-site map (Fig. 1B, rectangular grey area) reveals that in *C. bicolor* the nest sites are distributed in a patch-like way. This aggregated distributional pattern corresponds with our previous finding that *C. bicolor* unlike *C. fortis* exhibits a polydomous colony structure (Wehner et al., 1983; Schmid-Hempel, 1984). The queenright (primary) nest is associated with a number of queenless satellite (secondary) nests. At the peak of the activity period, colonies of *C. bicolor* comprise, on average, 3.2 simultaneously active nests (90 colonies, 292 nests, median: 3, quartiles: 1 and 4, maximum: 11; 4 years). The number of nests that have been active within a colony at least once during the entire foraging season amounts to 6.1 (55 colonies, 334 nests, median: 5, quartiles: 2 and 9, maximum: 15; 2 years). The secondary nests are connected to the queenright

Table 3. Carrier transport distances in *C. bicolor* as recorded during the peak period of satellite nest building (May to July). The table contains all nest to nest distances of observed carrier transports during the nest mapping periods in the *C. bicolor* study site. The distribution of carrier distances is skewed in the direction of longer distances. The longest observed carrier distances exceed even the mean nearest neighbour colony distances. This exemplifies the extreme plasticity and variability of the spatial layout of *C. bicolor* colonies

Year	N	Median Distance [m]	1. Quartile Distance [m]	3. Quartile Distance [m]	Maximum Distance [m]
1987	38	7.31	3.28	11.24	31.47
1988	10	3.00	1.74	3.82	16.35
1989	89	7.39	3.56	16.38	64.81
1990	16	5.80	2.97	7.51	23.02
1991	31	6.82	3.68	10.09	50.88
total	184	6.66	3.33	11.89	64.81

Table 4. Distribution patterns of *C. bicolor* colonies as inferred from cluster analysis and observed inter-nest transport of individuals. The table presents the estimated number of “colonies” (Fig. 2) and the corresponding “colony densities” within the $3.5 \cdot 10^4$ m² test area (shaded frame in Fig. 4B). In performing the Nearest-Neighbour-Analysis the sites of a colony is computed as the arithmetic mean of the coordinates all nest entrances belonging to an inferred colony. For definitions and conventions see Table 1

Year	Colonies	Area [m ²]	Density [10^{-4} m ⁻²]	$r \pm sr$ [m]	$r_{th} \pm \sigma r_{th}$ [m]	R	c	P
1988	23	$3.5 \cdot 10^4$	6.6	30 ± 9	22 ± 3	1.38	3.16	0.001
1989	20	$3.5 \cdot 10^4$	5.7	29 ± 8	23 ± 3	1.25	1.92	0.027
1990	14	$3.5 \cdot 10^4$	4.0	33 ± 9	28 ± 4	1.17	1.06	0.142
1991	14	$3.5 \cdot 10^4$	4.0	39 ± 5	28 ± 4	1.38	2.41	0.008

nest and with each other by above-ground carrier transports (Table 3). As the *C. bicolor* nest sites shift considerably, that is, as existing satellite nests are often abolished and new ones are formed, the flow of carriers between two particular nests is often reversed in direction. Towards the end of the season many satellite nests are given up, so that the hibernating colony usually contains only one or very few nests.

Technically, the carrier transport (Table 3) can be used to establish the affiliation of particular nests to particular colonies (see arrows in Fig. 2) and to determine the nearest neighbour nest distances within a colony (73 nests, mean: 7.90 m, median: 5.78 m, quartiles: 2.69 m and 10.70 m, maximum value: 35.76 m; year 1989). By applying a cluster analysis in combination with the carrier-transport criterion we were able to transform the nest-site pattern of Fig. 1 B into the most likely colony-site distribution (Fig. 2). If the nearest neighbour analysis performed on the former (nest-based) pattern and presented in Table 2 is now repeated for the latter (colony-based) pattern, a striking difference results. Even though the R value again departs significantly from the random distribution hypothesis, it now does so in the opposite direction ($R = 1.30 \pm 0.10$; for year-by-year data see Table 4), i.e., towards a uniform distribution. Hence, the monodomous colonies of *C. fortis* and the polydomous colonies of *C. bicolor* exhibit the same kind of distribution. According to an ANOVA, the species differences present at the nest-site level (ANOVA for group effects – differences between nest maps – $F_{7,327} = 14.58$, $P < 0.001$ and orthogonal contrasts for species effects $F_{1,327} = 97.66$, $P < 0.001$) vanish at the colony-site level (ANOVA for group effects – differences between colony maps – $F_{7,183} = 0.0672$, $P > 0.10$ and orthogonal contrasts for species effects $F_{1,183} = 0.0145$, $P > 0.10$). In *C. bicolor* the R value for the colony pattern is even slightly higher than in *C. fortis*.

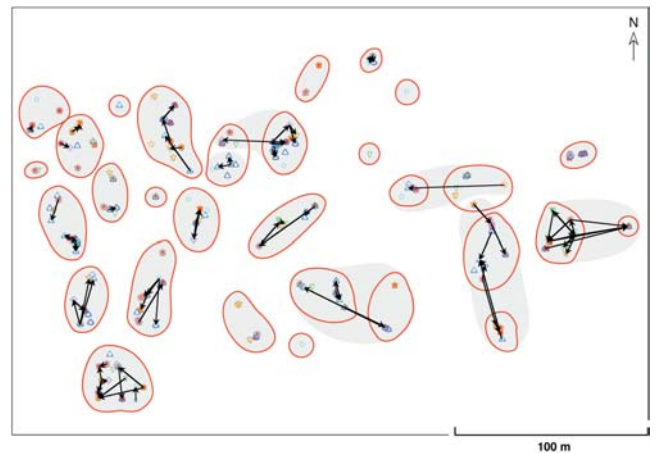


Figure 2. Map of inferred colonies of *C. bicolor* as recorded in 1989 (shaded areas). The map is based on nest entrance mappings in spring and summer. The shaded areas include all nest entrances of the polydomous colonies. The colony affiliations are deduced from a combination of observed “carrier transports” (arrows) and the results of an iterative clustering algorithm on the nest site pattern. The red line shows the iterative clustering process by 30 clusters. This number (30) led to the smallest amount of incompatibilities with the mappings derived from observed “carrier transports”. All ambiguities in colony affiliation that occurred between the cluster computations and the “carrier transport” data have been resolved in favour of the latter. Closed red symbols depict nest entrances active together at the peak of the foraging activity period end of June. Open symbols indicate nest entrances active either earlier or later in the same season

At the *bicolor* study site two other (smaller) *Cataglyphis* species, *C. albicans* and *C. ruber*, occur alongside *C. bicolor*. They reach high local nest densities (in the area shown in Fig. 3: $633 \cdot 10^{-4}$ m⁻² in *C. albicans*, $167 \cdot 10^{-4}$ m⁻² in *C.*

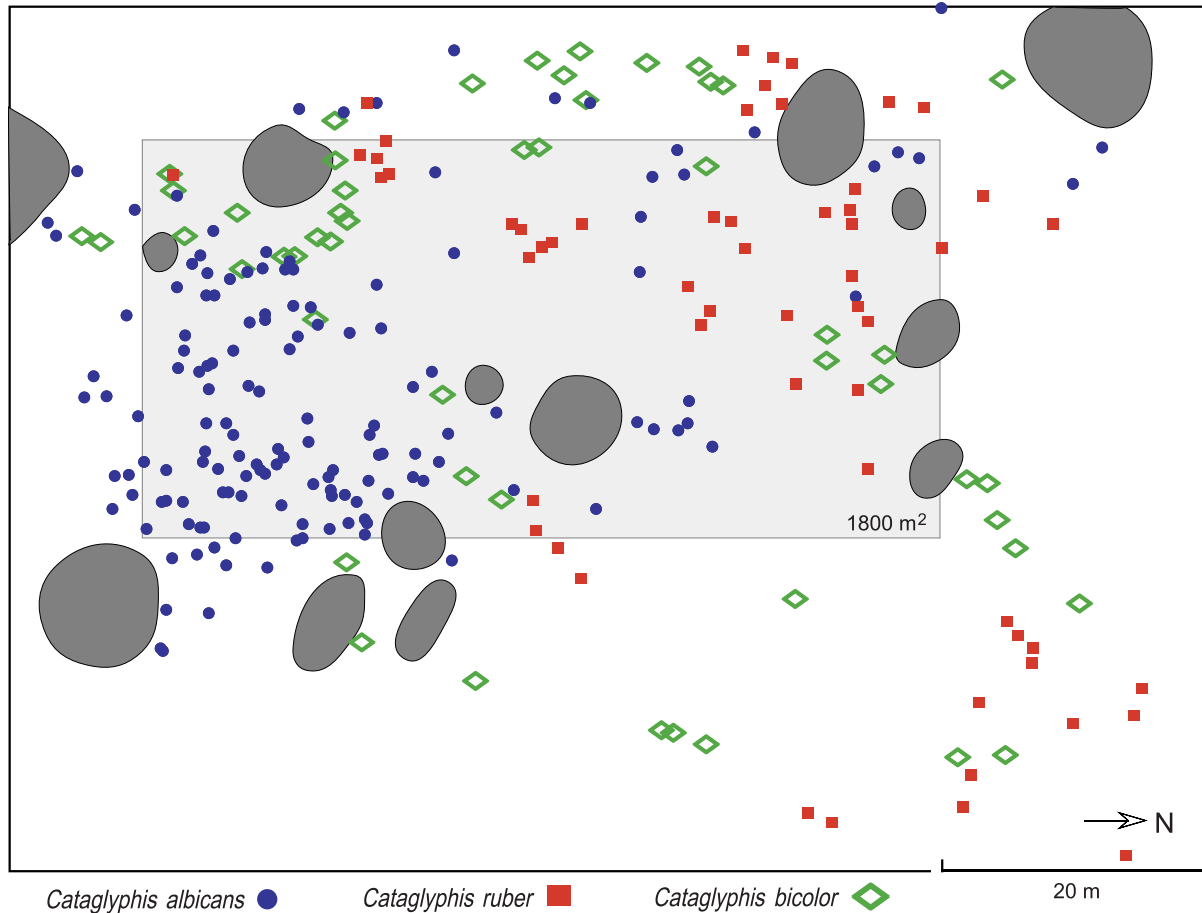


Figure 3. Nest site maps of three syntopic *Cataglyphis* species: *C. albicans*, *C. ruber* and *C. bicolor* (April–May 1988). The area is part of the ‘bicolor study site’ (see frame in Fig. 1 B). Larger thorn bushes, most of them *Nitraria retusa*, are marked as dark grey blobs

ruber, and $117 \cdot 10^{-4} \text{ m}^{-2}$ in *C. bicolor*; 1800 m², April 30, 1988), but rather than being homogenously distributed over the entire area, they form a patchwork of clusters of either *C. albicans* or *C. ruber* nests. Over a larger area the two small species together may reach a 10 to 20 times higher nest density than *C. bicolor* ($494 \cdot 10^{-4} \text{ m}^{-2}$, 4000 m² area and $31 \cdot 10^{-4} \text{ m}^{-2}$, 46'900 m² area, respectively; combined observations of all nests active during March–April 1988). All three species exhibit aggregated nest-site distributions ($R = 0.67$, *C. albicans*; $R = 0.55$, *C. ruber*; $R = 0.57$, *C. bicolor*) and polydomous colony structures, but do so on different spatial scales.

The difference between *C. bicolor* and *C. fortis* gets even larger, if one adds data on the sizes of the colonies and the body weights of individual ants to the data on colony densities. The colonies of *C. bicolor* contain 18 times more workers (3630 ± 2442 , $N = 8$ colonies) than the colonies of *C. fortis* (202 ± 125 , $N = 4$ colonies). As the body weight of a *C. bicolor* worker (23.0 mg, quartiles 14.6 and 31.7 mg, $N = 1693$) is 2.6 times that of a *C. fortis* worker (8.8 mg, quartiles 6.3 and 11.7 mg, $N = 103$), the habitat specific biomass of *C. bicolor* (42 kg per km²) exceeds that of *C. fortis* (0.5 kg per km²) by nearly two orders of magnitude. These habitat differences are increased even further, if the com-

combined biomass of *C. albicans* (10 kg per km²) and *C. ruber* (2 kg per km²) – the two *Cataglyphis* species occurring syntopically with *C. bicolor* at the *bicolor* study site – are included in the comparison.

2. Pattern dynamics

Monodomy in *C. fortis* and polydomy in *C. bicolor* are correlated with yet another parameter of population structure: its dynamic characteristics. We had already alluded to the pronounced intra-annual nest-site ‘fluidity’ within *C. bicolor* colonies. Now we can add a similar inter-annual effect. As systematic samplings of nest locations over periods of at least four consecutive years show, *C. fortis* and *C. bicolor* differ markedly in the long-term stability of their nest sites. The extreme stability underlying the nest-location maps of *C. fortis* (Fig. 4 A) contrasts sharply – as expected from the intra-annual fluctuation – with the amazing flexibility of the maps in *C. bicolor* (Fig. 4 B). In *C. fortis* each year 76.2 per cent ($N = 42$) to 84.4 per cent ($N = 32$) of the nests could be located at exactly the site of the previous year (or at a maximum 2-m distance from the former site). At least every tenth nest (9.4% of $N = 340$) lasted for at least 9 years.

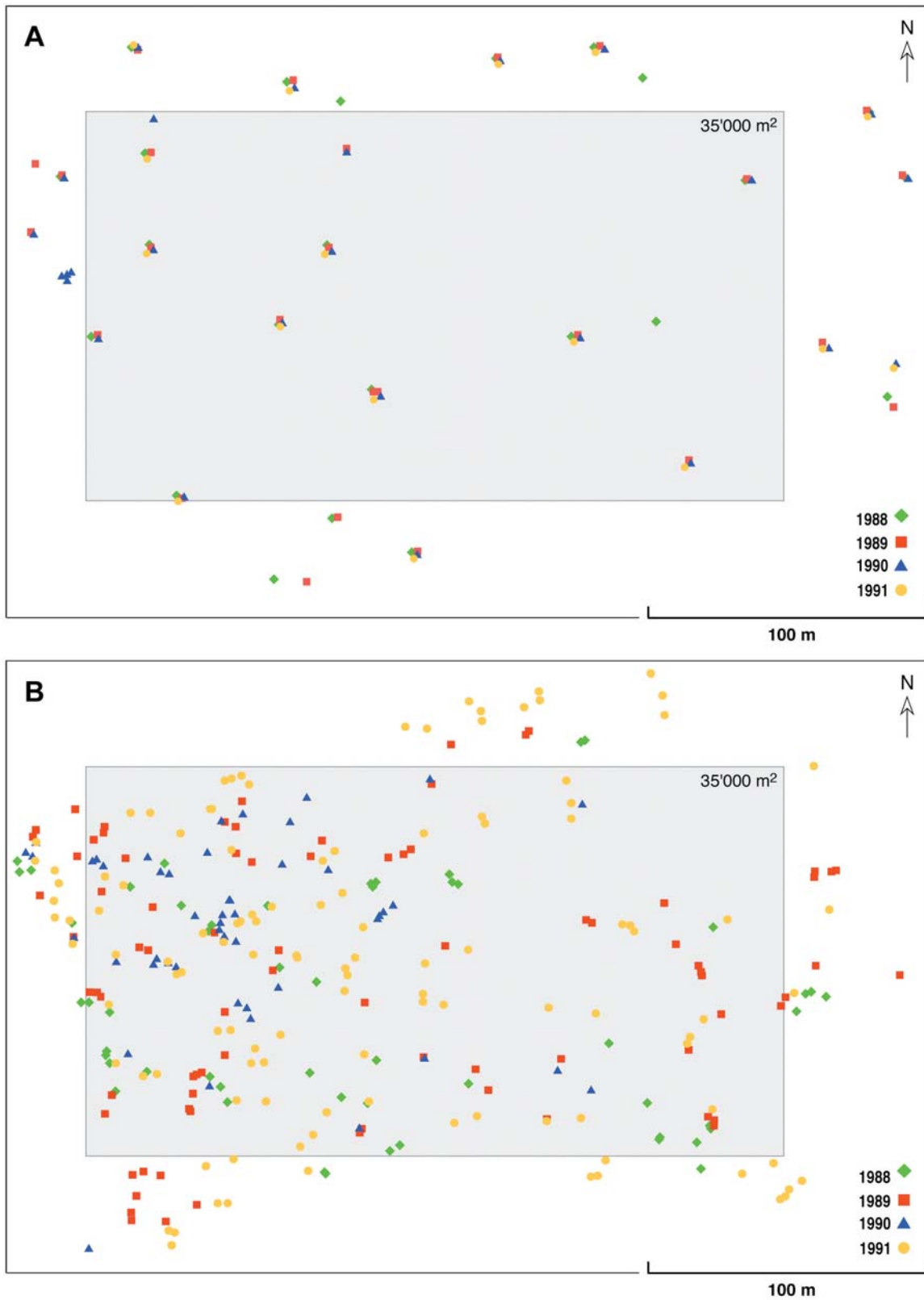


Figure 4. Nest sites maps of **A** *C. fortis* and **B** *C. bicolor* for a 4-year period (1988–1991): inter-annual variation.

All these values form lower limits, because in two consecutive years it was not always possible to distinguish between nests newly discovered by the observer and nests newly founded by the ants. In contrast, *C. bicolor* showed hardly any consistency in the locations of its nest sites between two mapping periods (years). In this species it was almost impossible to relocate nests at the same site at which they had been observed in the previous year. On average, this occurred in only 4.9 percent of the cases ($N = 139$). Nevertheless, in spite of the new nest-site arrangements every year, an ANOVA did not reveal any among-year differences in the distribution pattern of the *C. bicolor* nest sites (mean squares: 0.12 and 0.14, d. f. = 3 and 287, respectively; $F = 0.86$, $P > 0.10$).

Discussion

The most striking differences between the population structures of the two *Cataglyphis* species compared in the present account relate to population density (and hence the overall *Cataglyphis* biomass supported of the two species specific habitats) and population fluidity (and hence the spatio-temporal distributional patterns of the two species). Let us first deal with these two characteristics separately and then try to link them to each other and to the monodomy-polydomy aspect of the two species.

1. Population density and population structure

Sometimes particular nests of *C. fortis* and *C. bicolor* may be located only a few hundred meters apart from each other, but the habitats occupied by the two species are completely different: extremely food-impovertised salt flats in the case of *C. fortis* and nutritionally much richer low-shrub semi-deserts in *C. bicolor*. This difference in the nutritional value of the two interdigitated habitats is reflected in the nest density being 5.1 times higher in *C. bicolor* than in *C. fortis* (1535 ± 497 and 300 ± 42 nests per km^2 , respectively). As *C. bicolor* exhibits a polydomous colony structure (3.2 ± 2.4 simultaneously active nests per colony, 4 year mean), but *C. fortis* does not, the density of colonies and hence of egg-laying queens varies only by a factor of 1.7 between the two monogynous species (507 ± 128 and 300 ± 42 colonies per km^2 in *C. bicolor* and *C. fortis*, respectively). This ratio, however, completely underestimates the difference in the number of *Cataglyphis* individuals and, even more so, the difference in *Cataglyphis* biomass between the two North African habitats (see p. 191).

In spite of these large differences in population density, *C. bicolor* and *C. fortis* coincide in the spatial distribution patterns of their colonies. Both species exhibit a pattern that deviates highly significantly from randomness towards a uniform (over-dispersed) distribution. This is in contrast to the random distribution reported for *C. iberica*, a likewise monogynous and polydomous species studied by Cerdá et al. (2002) at two more mesic sites in south-east and north-east Spain (Murcia, 300 mm total annual rainfall; Barcelona,

600 mm total annual rainfall). There *C. iberica* reaches nest densities from 50 to $150 \cdot 10^{-4} \text{ m}^{-2}$ (Dahbi et al., 1997), similar to the nest density of *C. ruber* ($126 \cdot 10^{-4} \text{ m}^{-2}$) and intermediate between the nest densities observed for *C. bicolor* ($11 \cdot 10^{-4} \text{ m}^{-2}$) and *C. albicans* ($368 \cdot 10^{-4} \text{ m}^{-2}$) at our study site in the year 1988. In North Africa, however, even *C. fortis*, which occupies the poorest of all *Cataglyphis* habitats, where it reaches most probably the lowest of all *Cataglyphis* population densities, exhibits an over-dispersed spatial packing structure of its colonies and, hence, makes optimal use of its foraging ground.

As this dense packing structure ($R > 1$, Table 1 and Table 4) might let one assume, the mean nearest neighbour distances between nests, i.e. between colonies in the monodomy *C. fortis* and between nests of different colonies in the polydomous *C. bicolor*, are strongly correlated with the foraging ranges of the two species. In *C. bicolor* as well as in the closely related *C. nodus* in Greece (Platamon study site, Wehner et al., 1983) mean nearest neighbour distances r correspond rather well to the radius R_c of a circle drawn around the nest and defining the area in which the ants spend 90 per cent of their foraging time. The same holds true for *C. albicans* (Schmid-Hempel, 1983), even though in this smaller species r and R_c amount only to one third of the corresponding values in *C. bicolor*. In *C. fortis* search density plots of foragers and hence data on R_c are not yet fully available, but a first set of recordings of individual foraging runs clearly shows that in this species the mean foraging distances are much larger than in *C. bicolor* (Wehner, 1987).

Two further parameters that are correlated with foraging range and inter-nest distance are running speed and relative length of the legs (Wehner, 1983): the largest-legged though medium-sized *C. fortis* reaches the highest running speeds, exhibits the largest foraging distances and establishes the widest (but still uniform) inter-nest spacing pattern. Just the opposite, i.e. smallest foraging ranges and smallest inter-nest distances, applies to the smallest-legged *C. albicans*. In all four parameters mentioned above the largest of the three *Cataglyphis* species considered here occupies a middle position. Obviously, it is a number of functional-morphology traits related to the animal's locomotor behaviour that is correlated with, or has been adapted to, the foraging ranges of the workers and the distances between the foragers' central places, the nests.

The fact that the medium-sized *C. fortis* ranks highest in terms of foraging range, running speed, and inter-nest distance is certainly correlated with the poor nutritional value of its habitat, in which *C. fortis* is the only *Cataglyphis* species. In contrast, the surrounding nutritionally richer low-bush semi-desert is inhabited syntopically by the large-sized *C. bicolor* and the small-sized species *C. albicans* and *C. ruber* (Fig. 3). At Maharès the latter species reaches the northern limit of its distributional range, which extends into the central Sahara.

As all *Cataglyphis* species considered in the present account are generalist scavengers depending on the same type of food (arthropod carcasses) at the same time of day and year, strong competitive interactions are to be expected.

These interactions are nearly exclusively of an exploitative, i.e. scramble competition type (Wehner et al., 1983; Schmid-Hempel, 1983; Wehner, 1987; Dietrich and Wehner, 2003). In this state of affairs, it will pay any species to adopt particular food-retrieval preferences. For example, the frequency distributions of the sizes of the food items retrieved by *C. bicolor* and *C. albicans* deviate significantly from each other and from the size distribution of the food items available within the foraging ranges of the two species (Schmid-Hempel, 1983). This means that in the richer of the two habitats, at the *bicolor* study site, which supports a *Cataglyphis* biomass that is one hundred times higher than that of the *fortis* study site (see above), a large-sized and at least one small-sized *Cataglyphis* species differentially exploit the upper and the lower end of the food-size distribution. In contrast, in the poorer habitat only a single, medium-sized *Cataglyphis* species occurs: *C. fortis*, which has the entire range of food-sizes at its disposal. These correlations might also apply to the ecological equivalent of *Cataglyphis* in southern Africa, i.e. to ants of the myrmicine genus *Ocymyrmex*, which comprises a similar range and distributional pattern of small-, medium- and large-sized species (Wehner, 1987).

Levings and Traniello (1981) proposed a model for the interpretation and prediction of ant nest-site distribution patterns, based on the ants' foraging distances. The model predicts that if there is a partial niche overlap – as is the case in the sympatric *Cataglyphis* species – intra-species competition should be further increased relative to inter-species competition. As a consequence, regular patterns of nest-site distributions should result – as has been observed in the colony-site distributional pattern of *C. bicolor*.

2. Population fluidity and polydomy

C. fortis and *C. bicolor* do markedly differ not only in their population densities as discussed above but also in the stability/fluidity of their nest-site distributions. While in the former species these distributions are amazingly stable over periods of several – in some cases up to ten – years (Fig. 4A), *C. bicolor* exhibits a very dynamic colony regrouping system on an intra-annual and, consequently, all the more on an inter-annual time scale (Figs. 1B and 4B, respectively). This high temporal variability, which nevertheless maintains the aggregated spatial distribution of the nests within a colony and the over-dispersed distribution of the colonies within the population, is associated with the obligate polydomy of the species. Outside workers, mostly advanced foragers (Wehner et al., 1972), carry inside workers, pupae, larvae and eggs from one nest to another (Wehner et al., 1972; Duelli, 1976; Cerdá and Retana, 1992; Dahbi et al., 1997). The association of polydomous colony structure and high nest renewal rate was found and amply documented in the Spanish *C. iberica* as well (Cerdá et al., 2002). These authors describe interference competition between *C. iberica* and *Camponotus foreli*, in which *C. foreli* exhibits superior performances in fighting, whereas *C. iberica* does so in digging. This asymmetry leads to nest usurpation of *C. iberica* nests by *C. foreli*, and to nest

relocations by *C. iberica* (Cerdá and Retana, 1998). *C. fortis*, on the other hand, is strictly monodomous.

At first sight, the latter finding is surprising. For it is especially under the constraints of large foraging distances that ant species have been reported to develop polydomous colony structures, in order to increase foraging ranges and hence colonywide food intake rates. For example, *Formica polyctena* can establish temporary 'way stations' between the nest and a food source. Later these way stations often develop into satellite nests (Mabelis, 1979). In the Malaysian *Dolichoderus cuspidatus* (Maschwitz and Hänel, 1985) and the Argentine ant *Linepithema humile* (Hollway and Case, 2000) new nests are established at sites located close to food areas, especially when foraging distances have become too large. Colonies of fire ants, *Solenopsis invicta*, have been observed to occupy foraging areas prior to budding off sister colonies in these areas (Showler et al., 1990). The tropical giant ant *Camponotus gigas* even employs specialized transporter ants to carry food from peripheral nests to the central nest containing the queen. In addition, it establishes intricate communication systems, which enable several nests of a colony to cooperate in foraging by triggering waves of recruitment, which spread from the nest nearest to the food source to nests farther apart (Pfeiffer and Linsenmair, 1998). In all these examples of 'dispersed central-place foraging' (McIver, 1991) transport capacity and hence foraging yield are optimized by minimizing travel time and hence foraging costs.

Seen in this light, one might wonder why *C. fortis* has not adopted the polydomy mode of colony structure. As it has not, its foragers must travel much larger distances within a much poorer habitat than foragers of the polydomous *C. bicolor* have to do. Probably there is a threshold number of colony members to make the establishment of satellite nests favourable. Anecdotal observations of short term satellite nest foundations for only one or two weeks in a big *C. fortis* colony in 1989 – also the year with the highest observed nest density of this species – could point in this direction. Our results are in accordance with the hypothesis (Dahbi et al., 1997) that polydomy may be linked with high nest densities. Seasonal polydomy under high nest densities could help to reduce disease and parasite load, but there is no evidence yet for such a function in our North African *Cataglyphis* populations.

Any more definitive answer to the question of why *C. fortis* with its widely dispersed colonies is monodomous must await more comparative data on efficiency rates of individual foragers, on predatory risks of workers while foraging, i.e. risks resulting from robber flies, spiders, tiger beetle larvae, etc., and finally on colony-targeted attacks by predators, e.g. by subterranean doryline ants. The latter (defensive) role of polydomy – spreading the risk of predation – has been discussed and observed most directly by Droual (1984) for *Pheidole desertorum*, in which a colony avoids approaching predators by frequently shifting from one nest site within a set of multiple nests to another, but by occupying only one of these nests at any one time. Two subterranean *Dorylus* species (*D. fulvus* and *D. atriceps*) occur in our study area, and over the years we have observed several attacks of these

species of driver ants on *C. bicolor* colonies. At least one of these episodes was followed by a relocation of the attacked *C. bicolor* nest. Finally, it is a social function that has been ascribed to polydomy: workers can increase their inclusive fitness by rearing brood apart from their own mother queen in queenless satellite nests (e.g. Snyder and Herbers, 1991; Partridge et al., 1997). In fact, in *C. iberica* (Cerdá et al., 2002) as well as in *Camponotus gigas* (Pfeiffer and Linsenmair, 1998) virgin females have never been found in the central (queenright) nests of these monogynous and polydomous species. Why, then, has *C. fortis* opted for monodomy? Nest location and/or construction in the comparatively wet salt-pan environment might be a factor that contributes to counter-balance the ecological and social selection pressures favouring a polydomous colony system. As studies in morphometric and molecular systematics show (Wehner, 1983; work in progress by the *Cataglyphis* systematics group), *C. fortis* is related most closely to *C. albicans*, which is polydomous (Schmid-Hempel, 1983) and from which it might have split off in adaptation to the North African salt-pan type of habitat (Wehner, 1983). Hence, in *C. fortis* monodomy is certainly a derived character. Whatever the adaptive significance of the *C. fortis* monodomy might be, the strict monodomy-and-temporal-stability syndrome of colony structure in *C. fortis* contrasts sharply with the polydomy-and-temporal-variability syndrome in *C. albicans* and *C. bicolor*.

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