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Spatial patterns, temporal variability, and the role of multi-nest colonies in a monogynous Spanish desert ant

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Abstract. 1. The colonies of the Spanish desert ant *Cataglyphis iberica* are polydomous. This study describes the temporal and spatial patterns of the polydomy in this species at two different sites, and presents analyses of its role in reducing the attacks of the queen over sexual brood, and in allowing better habitat exploitation.

2. The spatial distribution of nests was clumped while colonies were distributed randomly. Mean nearest neighbour distance ranged from 3.4 to 7.0 m for nests and from 12.3 to 14.1 m for colonies. Distance of foragers searching for food varied among nests: mean values were between 6.1 and 12.6 m.

3. At both sites, the maximum number of nests per colony occurred in summer, during the maximum activity period of the species. Colonies regrouped at the end of this period but overwintered in several nests.

4. Nest renewal in *C. iberica* colonies was high and showed great temporal variability: nests changed (open, close, re-open) continuously through the activity season and/or among years. The lifetime of up to 55% of nests was only 1–3 months.

5. Polydomy in *C. iberica* might decrease the interactions between the queen and the sexual brood. In all colonies excavated just before the mating period, the nest containing the queen did not contain any virgin female. Females were in the queenless nests of the colony.

6. The results also suggest that polydomous *C. iberica* colonies may enhance habitat exploitation because foraging activity per colony increases with nest number. The relationship between total prey input and foraging efficiency and number of nests per colony attains a plateau or even decreases after a certain colony size (four to six nests). This value agrees with the observed mean number of nests per colony in *C. iberica*.

Key words. Ant, *Cataglyphis iberica*, foraging activity, foraging efficiency, habitat exploitation, nest distribution, polydomy.

Introduction

Ant nests have frequently been treated as spatially fixed structures. This fixedness of position, combined with an ability to exploit surrounding resources intensively, has led to parallels being established between ant colonies and plants (López *et al.*, 1994). Nevertheless, as Hölldobler and Wilson (1990) pointed out, a startling new picture has begun to emerge concerning the stability of ant colonies: ants move from one site to another more frequently than imagined previously (Smallwood, 1982a; Herbers, 1985; Tsuji, 1988; Gordon, 1992; Briano *et al.*, 1995). Instability of colonies may be influenced by both biotic and abiotic factors: many species abandon their nests when confronted by environmental changes (Carlson & Gentry, 1973; Smallwood, 1982a,b; Yamaguchi, 1992) or when attacked by other ants or predators (LaMon & Topoff, 1981; Droual, 1984; Yamaguchi, 1992). In other species, colonies overwinter

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as a unit then break up into nest fractions over the active season, coalescing again in the autumn (Herbers, 1986, 1989; Traniello & Levings, 1986; Snyder & Herbers, 1991; Banschbach & Herbers, 1999).

Social organisation of ant colonies varies greatly depending on the number of nests and the number of queens (or reproductive individuals). Ant colonies with multiple nests, usually in close proximity to one another, are termed polydomous. In most species, polydomy is linked to polygyny (e.g. Rosengren *et al.*, 1993; McIver *et al.*, 1997; Pedersen & Boomsma, 1999) but this correlation is very weak. In fact, many monogynous ant species are also polydomous (e.g. Snyder & Herbers, 1991; Liu *et al.*, 1998; Pfeiffer & Linsenmair, 1998), while several polygynous species are monodomous (e.g. Pearson, 1983; Pamilo & Rosengren, 1984; Pedersen & Boomsma, 1999). They are frequently polydomous species with some monodomous colonies or populations. Moreover, other species may have a variable social structure (Boomsma *et al.*, 1993; Herbers & Banschbach, 1999). In polygynous species, polydomy has been described as allowing a more efficient habitat exploitation (Cherix, 1981; Pamilo & Rosengren, 1984). In monogynous species, three different (but not necessarily exclusive) roles of polydomy have been suggested: an *ecological* role, a *social* role, and a *defensive* role. Ecologically, polydomy may reflect a strategy to increase foraging range and colony-wide food intake (Traniello & Levings, 1986): the system of allocating nests, workers, and brood throughout a colony's foraging area has the potential to increase foraging efficiency and competitive ability (Holway & Case, 2000). Polydomy may also have a social role by reducing the negative effect of the queen on the sexual brood (Snyder & Herbers, 1991; Banschbach & Herbers, 1996a,b): in most ant species, workers of queen-right nests attack and kill female larvae when they show signs of developing into queens but feed and rear these larvae when the queen is absent (see reviews by Brian, 1980, 1983; Hölldobler & Wilson, 1990). Finally, polydomy may also have a defensive role: a system of multiple nests may represent a defence technique against predators if ants abandon the attacked nests and reinstall their population in other nests of the same colony (Mabelis, 1979; Droual, 1984).

Colonies of the Spanish desert ant *Cataglyphis iberica* (Emery) are monogynous and polydomous. Links between different nests are maintained by the exchange of individuals through social carrying (Cerdá *et al.*, 1994), which serves to maintain colony cohesion (Dahbi *et al.*, 1997). Cerdá and Retana (1998) suggested that the occurrence of polydomous colonies in this species may represent a defensive technique to cope with the harassment of another ant species, *Camponotus foreli* Emery, the attacks of which against *C. iberica* nests usually conclude with the deaths of many workers of both species, and with nest abandonment by *C. iberica*. Nevertheless, these harassment episodes between the two species are a rather rare and unpredictable phenomenon (Cerdá & Retana, 1998). It is difficult to imagine that such a complex polydomous system could have been developed solely for this defensive function, especially considering that *C. iberica* colonies are always polydomous, even in broad areas where *C. foreli* is absent. The aim of the study reported here was to analyse the temporal and spatial patterns of the polydomous system of *C. iberica* and to test whether polydomy also has a social role (i.e. in reducing the negative effect of the queen on the sexual brood) and/or an ecological role (i.e. in allowing better habitat exploitation and increasing colony foraging areas and colony food intake) for *C. iberica* colonies.

Materials and methods

The species: Cataglyphis iberica

Cataglyphis iberica is an endemic ant in the Iberian Peninsula. It is a thermophilous species that nests in semi-arid environments without tree canopy and with scant vegetation. Workers search for and transport animal remains, mainly arthropod corpses, individually. Nest structure of this species is quite simple (Cerdá, 1989; Plaza & Tinaut, 1989): there is always a single nest entry, which leads to a superficial gallery, connected to a vertical gallery 40–70 cm in depth, where all chambers and secondary galleries of the nest connect. Colonies are monogynous and polydomous; the only queen lives in the nest termed the *central nest* because it has more workers and higher adult transport and foraging activity than do the other nests (Cerdá *et al.*, 1994). Although colonies may exceptionally have up to 14 nests, the mean (± SE) number of nests per colony is 4.2 ± 0.5 ($n = 20$). Nest population is between 150 and 800 workers, while colony population ranges from 500 to 2500 workers.

Field study sites

Field observations were carried out at two sites. The La Paloma site, Murcia, south-east Spain (37°50′N, 1°5′W) is a dry plain without trees but with a few shrubs. The local climate is semi-arid, with mean annual temperature of 18.6 °C and total annual rainfall of 308 mm. The Bellaterra site, north-east Spain, is located on the campus of the Autonomous University of Barcelona (41°21′N, 2°3′E, 600 km from the La Paloma site). Tree canopy is absent, and the only dominant shrub is *Inula viscosa* Aiton. The local climate of this site is Mediterranean, with mean annual temperature of 15.2 °C and total annual rainfall of 607 mm. In Bellaterra, observations were carried out mainly at two plots: plot 1 (2000 m^2) and plot 2 (500 m^2). Other plots, plot 3 (2000 m^2), plot 4 (1500 m^2), and plot 5 (500 m^2), were used sporadically. All plots had similar vegetation and soil composition.

Spatial distribution of nests and colonies

Spatial distribution patterns of nests and colonies were analysed by mapping all *C. iberica* nests and colonies in the

La Paloma site. Five mappings were carried out, in June 1986, June 1987, September 1987, August 1989, and August 1994. The total area mapped was 11 000 m^2 in 1986 and 1987 and 5000 m^2 in 1989 and 1994, because part of the initial plot had been urbanised. In this part of the study, individual colonies and nests were not followed from one sampling period to the next because the interest was in determining overall distribution patterns.

In each sampling period, all colonies and nests were sampled exhaustively and mapped. Active nests were located by offering a piece of biscuit to workers and following them to the nest. Maps were considered complete when no new nest was found after a sampling day (two or three observers, 4 h per day). The limits of the polydomous colonies were established by aggression tests, following the protocol described by Retana and Cerdá (1995). In each of these tests, a single worker from one nest was put together with four or five workers from another nest in a circular plastic box (6 cm diameter) coated on the inner walls with mineral oil in order to prevent escape. During the first 15 min following placement of the ants in the box, the interactions among them were noted and the states of the workers were recorded. Due to the high closure of *C. iberica* colonies (Dahbi *et al.*, 1996), when the two nests belonged to different colonies, the result of their interaction was strong and instantaneous aggression among workers. When the two nests belonged to the same colony, workers performed antennal inspection, social investigation, and even allogrooming.

The Clark and Evans (1954) statistical test of nearest neighbour distance was used to analyse spatial distribution patterns of *C. iberica* nests and colonies. This is based on the observed mean distance rA from each point to its nearest neighbour: small values of rA indicate an aggregated distribution of points, large values indicate regularity. The Clark and Evans statistic is calculated as the ratio R of the observed mean nearest neighbour distance rA to the mean nearest neighbour distance expected for a randomly distributed population rE. Because the distribution of the test statistic assumes an absence of edge effects, rE and standard error of rE were calculated according to Sinclair (1985) to correct for edge effects. Such effects occur because points closer to the boundary tend to have larger nearest neighbour distances than those well inside the boundary. The Sinclair estimates have a standard normal distribution for $n > 7$, and are regarded as a reliable approximation of a normally distributed index in most situations (Diggle, 1983). The nearest neighbour distance between colonies was estimated as the distance between the two nearest neighbour nests from a different colony. Statistical differences between mean nearest neighbour distances of nests (or colonies) among sampling periods were analysed using one-way ANOVAs. The individual values were then compared using a *post hoc* test (Fisher's protected least significant difference), where replicates in each period were the different mean nearest neighbour distances measured between nests (or colonies). Inspection of residuals was carried out to check for normality and homoscedasticity but no data transformation was needed.

Temporal variations in nest distribution and colony composition

Temporal variations in the distribution and composition of polydomous colonies (i.e. disappearance of nests and appearance of new nests) were analysed at Bellaterra sites 1 and 2. All active nests and colonies in each site were mapped monthly from June 1985 to June 1988 (during the activity season of the species, March–October). Mapped nests were marked with stones. Nest entrances did not vary in position by more than a few centimetres from one month to the next; this constancy made it possible to monitor them individually. Twenty mappings were made at each site. To analyse intra-annual differences in mean nearest neighbour distance, three periods of the year were considered: post-hibernation (March to the beginning of May), foraging period (mid May to August), and pre-hibernation (September and October). Statistical differences in mean nearest neighbour distance among periods and between sites were analysed using a two-way ANOVA.

Changes in the number of active nests at each site were evaluated using two indices: a renewal index (RWI, the percentage of new nests that had appeared in a sample), calculated as $\mathrm{RWI} = (N_i/T_i) \times 100$, where N_i was the number of new nests that appeared in sampling i (those nests that were not present in sampling $i-1$), and T_i was the total number of nests counted in sampling i; and a remaining index (RMI, the percentage of nests remaining from the previous sampling), calculated as $\mathrm{RMI} = (R_i/T_{i-1}) \times 100$, where R_i was the number of nests from sampling $i-1$ that remained in sampling i, and T_{i-1} was the total number of nests counted in the previous sampling ($i-1$).

Two-way ANOVAs were used to investigate differences between sites and among time periods for the different parameters examined: number of nests, renewal index, and remaining index. Renewal index and remaining index values were arcsin-square-root transformed. When there were no significant differences across sites, data were pooled for *post hoc* tests. A Fisher's protected least significant difference was used to separate means in one-way ANOVAs.

The lifetime of each nest was defined as the number of natural months elapsed from nest opening (the first evidence of activity in a new nest) to nest closure (the last evidence of activity). For nests that closed during the activity season, the re-opening rate was calculated as the time elapsed between the month of nest closure and the month of re-opening.

To determine variations in colony population in different periods of the year, *C. iberica* colonies were excavated in different months in the surroundings of the Bellaterra sites. All adults and brood were collected and later counted in the laboratory. Differences in colony population among periods (post-hibernation, foraging period, pre-hibernation) were analysed using one-way ANOVA. To evaluate whether polydomy might represent a mechanism to reduce the negative effect of the queen on the sexual brood, the presence of the queen and sexuals in the different nests of the 10 colonies excavated just before the mating period was noted carefully.

Foraging activity

Foraging activity of *C. iberica* colonies was studied in three colonies at the Bellaterra site in June, July, and August 1987 (one sampling day per month, only on sunny, hot days). Activity was measured during the hottest hours of the day (11.00–13.00 hours, period of maximum daily foraging activity) by counting exits and entries (both loaded and unloaded foragers) of workers in each nest for 5 min in each hour. The sum of the hourly number of exits and entries of all nests of each colony was used as an activity index for this colony. The number of prey collected by each colony was calculated as the sum of the loaded entries in each nest. Foraging efficiency (FE) of each active nest was calculated as: FE = (number of loaded workers/total number of returning workers) × 100. Mean foraging efficiency values were calculated for each colony. Data from each month and colony were considered as independent points for statistical analysis because colonies changed in both nest number and location from one month to another.

Foraging trips of *C. iberica* foragers were monitored in July 1995 in four nests of two colonies (colonies A and B, two nests each) at Bellaterra site 1. Thirty foragers per nest, leaving the nest between 11.00 and 13.00 hours (maximum daily activity period), were followed until they went no further, began a sinuous and short-distance search, and returned to the nest, either with or without prey. Linear foraging distance (and orientation) was measured as the direct path from the nest entrance to the most distant point attained by the worker (Cerdá & Retana, 2000). Foraging overlap was estimated from the same data set. To evaluate whether or not foragers avoided the proximity of other nests of the colony in their searching paths, the whole surface around each nest in the two colonies (A and B) was divided into eight 45° sectors. Foraging trips of workers from each nest were grouped in these sectors according to the direction of the most distant point in the path. Matched-pair comparisons (Wilcoxon test) of the number of workers of the two nests of the colony foraging in the eight directions were carried out for the two colonies separately.

Results

Spatial distribution patterns and nearest neighbour distances

Statistics for mean nearest neighbour distance for the La Paloma site are summarised in Table 1. Nests were clumped in all sampling periods. Differences of mean nearest neighbour distance of nests among sampling periods (Table 1) were not significant (ANOVA $F = 0.87$, d.f. = 4, P = NS). Only in 5.2% of cases (9 of 173), did the nearest neighbour nest belong to a different colony. *Cataglyphis iberica* colonies showed a pattern without significant differences from randomness (R not significantly different from 1 in any sampling period). Mean nearest neighbour distance among colonies did not differ significantly among sampling periods (ANOVA $F = 0.55$, d.f. = 4, P = NS).

Table 1. Statistics of mean nearest neighbour distances (MNND) calculated for *Cataglyphis iberica* nests and colonies at the La Paloma site. n = number of distances measured. R (coefficient of Clark & Evans, 1954) values significantly below 1 indicate clumping (aggregation) while values significantly above 1 indicate regularity (overdispersion). Significant differences of R from 1 (random distribution): *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, NS not significant.

Date	Density (nests per ha)	n	MNND (m)	R
Nests				
June 1986	36.3	28	5.1	0.54***
June 1987	50.6	37	4.4	0.56***
September 1987	60.8	41	3.8	0.62***
August 1989	63.9	30	4.0	0.59***
August 1994	76.5	26	5.0	0.81*
Colonies				
June 1986	13.6	13	14.1	0.89 NS
June 1987	20.9	22	13.6	1.10 NS
September 1987	21.8	23	12.6	1.05 NS
August 1989	21.9	11	12.3	1.04 NS
August 1994	20.0	10	13.6	0.99 NS

Temporal variations in colony distribution and composition

Differences in mean nearest neighbour distance for the two Bellaterra sites were significant ($F = 19.8$, d.f. = 1, $P < 0.001$), as were differences among years ($F = 2.83$, d.f. = 3, $P < 0.05$) and the interaction between the two factors ($F = 3.27$, d.f. = 3, $P < 0.05$). At Bellaterra site 1, mean nearest neighbour distance decreased from 1985 to 1988, while at site 2, it remained more or less similar among years (Fig. 1). In the two-way ANOVA used to analyse statistical differences in mean nearest neighbour distance among periods and between sites, intra-annual differences were found (ANOVA, $F = 5.0$, d.f. = 2, $P = 0.05$): the lowest mean

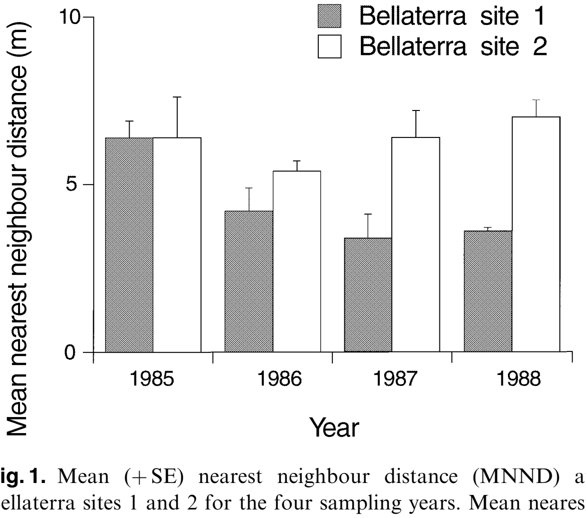

Fig. 1. Mean (+SE) nearest neighbour distance (MNND) at Bellaterra sites 1 and 2 for the four sampling years. Mean nearest neighbour distance at each site was calculated as the average value for the months sampled that year ($n = 6$ months per year, except for 1985 and 1988, when $n = 3$).

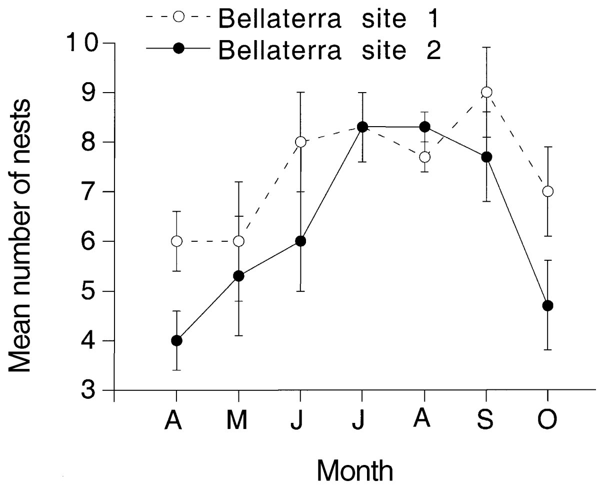

Fig. 2. Mean (± SE) monthly number of active *Cataglyphis iberica* nests each month during the activity period at the Bellaterra sites ($n = 3$ years).

nearest neighbour distance values were observed during the foraging season (mean ± SE: 4.7 ± 0.3 m), compared with similarly high values for post-hibernation (6.0 ± 0.8 m) and pre-hibernation (6.3 ± 1.0 m). The interaction between site and season was not significant ($F = 1.2$, d.f. = 2, $P =$ NS).

This process of regrouping nests during hibernation is also consistent with the fact that the number of workers per nest varied among seasons (ANOVA $F = 3.84$, d.f. = 2, $P < 0.05$): pre-hibernating (autumn) and post-hibernating (late winter–early spring) nests contained a greater number of workers (mean ± SE: 621 ± 81 workers for pre-hibernating nests, 698 ± 99 workers for post-hibernating nests, $n = 9$ and 8 respectively) than did nests excavated during the active period, i.e. spring and summer (414 ± 60, $n = 24$).

A two-way ANOVA was applied to the data from number of nests sampled each month at the two Bellaterra sites. Differences between sites were significant ($F = 8.6$, d.f. = 1, $P < 0.01$), as were differences among months ($F = 5.8$, d.f. = 6, $P = 0.001$), while the interaction between these factors was not significant ($F = 0.3$, d.f. = 6, $P =$ NS), indicating that differences among months remained consistent between sites. At both sites, the greatest number of nests was found in July, August, and September, and the lowest number in April and October (Fig. 2).

From one month to the next, several nests disappeared while others were newly excavated. The remaining index varied from 37 to 100% and the renewal index varied from 0 to 57%. For remaining index, there were no significant differences between sites or among months, and the interaction between these two factors was not significant ($F = 1.3$, 0.1, and 0.6 respectively, d.f. = 1, 6, and 6, all $P =$ NS). The renewal index showed significant differences among months ($F = 3.2$, d.f. = 6, $P < 0.05$) but not between sites ($F = 0.1$, d.f. = 1, $P =$ NS), and the interaction between site and month was not significant ($F = 1.9$, d.f. = 6, $P =$ NS). The maximum renewal index values were found for spring and early summer, and the lowest for autumn (Fig. 3). According to these results, the mean lifetime of nests was very low, 6.8 ± 1.0 months (mean ± SE, $n = 74$). More than 55% of nests were opened during fewer than 3 months (during the period of maximum activity, from June to August) while only 18.9% of nests were active in more than one foraging season (i.e. > 12 months). Nevertheless, re-opening of nests was also a relatively frequent phenomenon: 43% of closed nests (26 of 60 cases) re-opened at least once, and in some cases, twice or even three times. The time from nest closure to re-opening varied considerably: the most common result (17 of 26 cases: 65.4%) was for nests to re-open 6–7 months after closure (i.e. after a hibernation season), although two nests took 12 months to re-open.

Foraging activity

There was a positive, statistically significant linear relationship between number of nests per colony and activity index of each colony ($r^2 = 0.75$, $P < 0.001$, $n = 9$; Fig. 4a). There was also a positive, sigmoid relationship between prey collection rate and number of nests per colony ($r^2 = 0.87$, $P = 0.005$, $n = 9$; Fig. 4b), and a positive second-degree polynomial relationship between mean foraging efficiency and the number of nests per colony ($r^2 = 0.79$, $P = 0.005$, $n = 9$; Fig. 4c). The two curves shown in Fig. 4b and 4c improve considerably the amount of variation explained by a straight linear regression ($r^2 = 0.61$ and 0.25 respectively, both $P = 0.005$).

Foraging distances of *C. iberica* are shown in Table 2. Mean foraging distances of *C. iberica* workers at Bellaterra site 1 ranged from 6.1 to 12.6 m. Differences between colonies in mean foraging distance were not significant

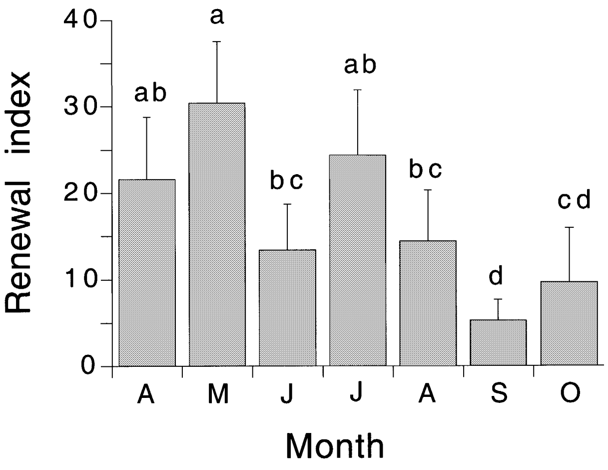

Fig. 3. Mean (+ SE) monthly values of the renewal index during the activity period of *Cataglyphis iberica*. Because differences between sites were not significant, data from the two Bellaterra sites were pooled ($n = 6$). Different letters indicate significant differences among periods according to the Fisher PSLD *post hoc* test.

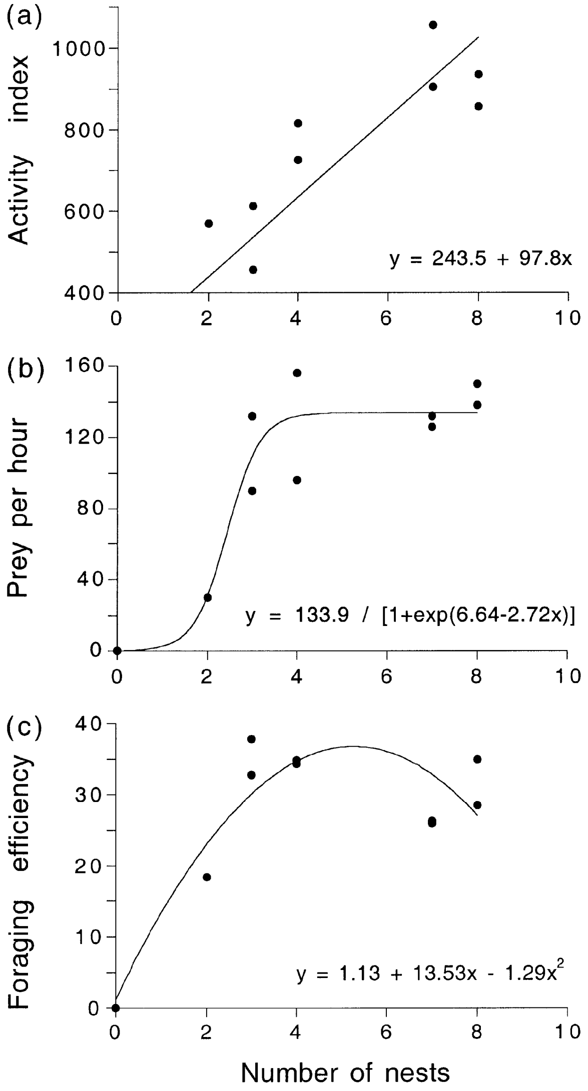

Fig. 4. Relationship between number of nests and (a) foraging activity of colonies (activity index: sum of entries and exits per hour), (b) colony prey input per hour, and (c) mean foraging efficiency. Colony means were calculated from nest values. Foraging efficiency was estimated as the percentage of loaded workers in relation to the total number of workers returning to the nest. The values in each figure have been fitted to a linear, a positive sigmoidal, and a second-degree polynomial function respectively.

Table 2. Foraging distances (mean ± SE and maximum) of *Cataglyphis iberica* workers from four nests during their seasonal maximum activity period. % > MICD = percentage of runs that attained a distance longer than the mean inter-colonial distance of 14.5 m (see Results). $n = 30$ workers for each nest.

		Foraging distance		
Colony	Nest no.	Mean ± SE	Maximum	% > MICD
A	1	12.3 ± 1.2	24.9	40.0
	2	6.1 ± 1.3	36.2	6.7
B	1	9.4 ± 0.8	20.5	10.0
	2	12.6 ± 0.8	21.2	30.0

(nested ANOVA $F = 2.95$, d.f. = 1, $P = \text{NS}$), but differences among nests (nested within colony) were significant (nested ANOVA $F = 11.0$, d.f. = 2, $P < 0.001$). Maximum distances ranged from 20.5 to 36.2 m. The percentage of workers that exceeded the largest mean inter-colony distance obtained from Table 1 (i.e. 14.5 m) was between 6.7 and 40.0%, depending on the nest (Table 2). Although individual paths were not mapped, field observations indicated that foragers from different colonies co-existed in large areas without apparent aggression, and that encounters were very rare and always resulted in immediate escape of both workers. In fact, workers did not avoid the proximity of other nests in their food-searching paths, because they foraged indiscriminately in sectors in the direction of or away from another nest in the colony (Wilcoxon signed rank test, $P > 0.5$ in all cases).

Composition of queen-right and queenless nests

In the excavated *C. iberica* colonies, central nests, which contained the only queen of each colony, had a significantly greater number of workers than did queenless nests (Student *t*-test, $t = 2.45$, $P = 0.01$; mean ± SE: 622 ± 90 workers for central nests, 379 ± 52 workers for queenless nests, $n = 15$ and 19 respectively). In none of the colonies excavated just before the mating period ($n = 10$) did the central nest contain virgin females or males, which were usually present in other queenless nests of the colony (Table 3).

Discussion

The polydomous colonies of *C. iberica* are a very dynamic system that shows large inter- and intra-annual variations. Nest opening and closing is frequent, with old nests being abandoned and new nests being excavated throughout the activity season. The lifetime of up to 55% of nests was only 1–3 months. This short lifetime could be considered a waste of energy invested in nest excavation. Nevertheless, due to the simple nest structure (Plaza & Tinaut, 1989) and the high capacity in this species for nest excavation (Cerdá & Retana, 1998), the activity is not very time consuming and may not be energy consuming; moreover, on many occasions, abandoned nests are re-occupied by the colony. Seasonal variations in colony composition of *C. iberica* differ considerably from those of other polydomous species. Many seasonally polydomous species (either monogynous or polygynous) have multiple nests during the active season but overwinter with the whole colony population regrouped in a single nest (Mackay & Mackay, 1983; Herbers, 1986, 1991; Tsuji, 1988; Snyder & Herbers, 1991). In *C. iberica*,

Table 3. Composition (queen, workers, females, males) of queenright and queenless *Cataglyphis iberica* nests of colonies excavated in June, just before the mating period of this species. $n = 10$ colonies.

Colony	Nest no.	Queen	Workers	Females	Males
1	1	Yes	182	–	–
	2	No	210	12	1
	3	No	176	5	–
	4	No	199	–	–
2	1	Yes	235	–	–
	2	No	256	70	8
3	1	Yes	431	–	–
	2	No	140	4	2
4	1	Yes	256	–	–
	2	No	269	3	–
5	1	Yes	500	–	–
	2	No	221	13	1
6	1	Yes	623	–	–
	2	No	231	18	14
7	1	Yes	402	–	–
	2	No	188	5	–
8	1	Yes	555	–	–
	2	No	453	11	1
9	1	Yes	701	–	–
	2	No	234	3	–
	3	No	289	3	–
10	1	Yes	778	–	–
	2	No	423	6	2
	3	No	311	5	7
	4	No	134	–	–

the maximum number of nests is also found during the maximum activity season, but colonies of the species are physically fractionated during overwintering. The links between the nests of the same colony are re-established in spring by means of intense adult transport traffic (Cerdá *et al.*, 1994; Dahbi *et al.*, 1997). In this period (spring and early summer), the renewal index is also highest (Fig. 3), i.e. the highest proportion of new nests is opened during these months.

Concerning the spatial patterns of *C. iberica*, the results shown in Table 1 indicate that nests are aggregated, which is the expected pattern for polydomous species. Nests in an ant colony are assumed to be modules and may be distributed as a way to expand the area over which a colony collects food resources by dispersing foragers, in order to avoid redundant search (Traniello & Levings, 1986). Traniello and Levings considered that, to avoid redundant foraging, nest entrances should be overdispersed and located at intervals equal to twice the average distance over which a forager can retrieve prey. This is not the case for *C. iberica*: the colonies have their nests aggregated with mean distances to nearest neighbour nest lower than foraging distances. Workers can forage in proximity to other nests or colonies and overlap with non-nestmates on their foraging trips. In poor habitats, colonies of other species have a tendency to develop a dense network of nests for maximum exploitation of territory (Czechowski, 1975). On many occasions, polydomous colonies move or split a new nest by budding to be closer to feeding sites (Mabelis, 1979; Maschwitz & Hänel, 1985; Showler *et al.*, 1990). The present results suggest that nest placement in polydomous *C. iberica* colonies may enhance habitat exploitation because foraging activity (i.e. number of foragers) per colony increases linearly with nest number. Nevertheless, the relationships between total prey input and foraging efficiency per colony and number of nests follow a sigmoid and a second-degree polynomial function respectively. Adler and Gordon (1992) developed a mathematical model to show how efficiently an ant colony discovers events occurring randomly in space and time (e.g. arthropod corpses, the main food resource of *C. iberica*). Their conclusion was that more ants find more such events but that efficiency of networks (a network of nests in the case of *C. iberica*) increases slowly and even decreases after a certain network size. Why is this so? Searching trips of workers are random. At low nest numbers, more searchers leaving from different starting points (nests) enhance the probability of the colony finding prey. When nest number increases, however, forager density and overlap of foraging trips also increase, lessening the probability of success. According to the relationships shown in Fig. 4, colony efficiency in *C. iberica* (considered as either the prey input or the percentage of workers arriving with prey) increases until the number of nests per colony is four to six, after which both variables asymptote or even decline with increasing numbers of nests. This result agrees with the observed mean number of nests per colony (4.2) in the colonies excavated during this study.

Together with this ecological role of polydomy in *C. iberica*, results from the excavated nests during the pre-swarming period suggest that polydomy in this species may also have a role related to the sexual brood, as occurs in other monogynous and polydomous species (Snyder & Herbers, 1991; Banschbach & Herbers, 1996a,b). In *C. iberica* colonies, sexual larvae and adults are always absent from the nest containing the queen, probably to prevent the queen from attacking them. This has been observed in laboratory colonies of a closely related species, *Cataglyphis cursor* Fonscolombe, in which the sole queen exerts an inhibition over workers, restricting their parthenogenetic egg-laying, and exerts a negative control over the sexual larvae by reducing their proteinous food supply and biting them directly, and over the male and female adults, by forcing the workers to attack and kill them (Retana & Cerdá, 1990, 1991). Nevertheless, the presence of males and virgin females in *C. iberica* colonies is limited to June, and nuptial flights take place from June to the beginning of July (X. Cerdá and J. Retana, pers. obs.), while the existence of a permanent polydomous social organisation occurs during the whole activity period of *C. iberica*. In *C. cursor*, which is a monodomous species during most of the year, there is a period of temporal polydomy, just before pre- and post-swarming events, to prevent queen attacks on sexuals (Lenoir *et al.*, 1988).

In conclusion, the advantages of polydomy for *C. iberica* colonies may be three-fold. As Cerdá and Retana (1998) suggested, a system of multiple nests may represent a homeostatic system for *C. iberica* colonies to resist attacks from predators or competitors, because it enables nests that suffer adverse events to be abandoned quickly. Moreover, results obtained in this study suggest that polydomy may also have a social function, because sexuals can be developed more easily in queenless nests, far from the influence of the queen. Nevertheless, both functions occur during very sporadic or short periods of the *C. iberica* life cycle, and the polydomous system is permanent during the whole year. Another function of polydomy, that related to habitat exploitation, may be important during most of the activity period. *Cataglyphis iberica* is a subordinate ant species specialised to discover food quickly in exploitative competition. It lives in dry and semi-arid habitats associated with low resource availability, and workers forage near their upper critical thermal limit, as occurs in most *Cataglyphis* species (Wehner *et al.*, 1992; Cerdá *et al.*, 1998; Cerdá & Retana, 2000). *Cataglyphis iberica* foragers search for food such as expanding tentacles or plant roots. In order to make the most of all available resources and to diminish the heat-shock risk for workers, a two-level system of tentacles is developed: the first level is composed of the foragers of each nest, while the second is composed of the nests of each colony. Then, *C. iberica* colonies with multiple nests have high foraging activity, and polydomy results in reduced total travel time of foragers (see also Pfeiffer & Linsenmair, 1998) and better habitat exploitation.

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