The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities

Abstract In this paper we test the influence of temperature and interference competition by dominant species on the foraging of subordinate species in Mediterranean ant communities. We have analyzed the changes in resource use by subordinate species in plots with different abundances of dominant ants, and in different periods of the day and the year, i.e., at different temperatures. The expected effects of competition by dominant species on foraging of subordinates were only detected for two species in the number of baits occupied per day, and for one species in the number of foragers at pitfall traps. In all three cases, subordinate species were less represented at baits or in traps in plots with a high density of dominants than in plots with a medium or low density of dominants. The number of workers per bait, and the foraging efficiency of subordinate species did not differ in plots differing in dominant abundance. Daily activity rhythms and curves of temperature versus foraging activity of subordinate species were also similar in plots with different abundance of dominant species, indicating no effect of dominants on the foraging times of subordinates. Instead, temperature had a considerable effect on the foraging of subordinate species. A significant relationship was found between maximum daily temperature and several variables related to foraging (the number of foragers at pitfall traps, the number of baits occupied per day, and the number of workers per bait) of a number subordinate species, both in summer and autumn. These results suggest that the foraging of subordinate ant species in open Mediterranean habitats is influenced more by temperature than by competition of dominants, although an effect of dominants on subordinates has been shown in a few cases. In ant communities living in these severe and variable environments, thermal tolerance reduces the importance of competition, and the mutual exclusion usually found between dominant and subordinate species appears to be the result of physiological specialization to different temperature ranges.

Key words Ant · Competition · Subordinate species · Temperature · Mediterranean communities

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Introduction

The role of competition in structuring communities has been controversial (Connor and Simberloff 1979; Strong et al. 1979; Connell 1983; Schoener 1983; Fowler 1986; Goldberg and Barton 1992, Gurevitch et al. 1992), but there are sound reasons, both theoretical and empirical, for considering interspecific competition to be important in shaping communities by determining which, and how many, species can coexist (Putman 1994; Begon et al. 1996). There is also considerable evidence that interspecific competition contributes to patterns of distribution and abundance in ant communities (Savolainen and Vepsäläinen 1988, 1989; Andersen 1992; Human and Gordon 1996; Morrison 1996). Ant species are organized in competitive dominance hierarchies where dominant species may outcompete subordinates (Fellers 1987; Savolainen and Vepsäläinen 1989). Strongly competitive ants, such as species of *Formica* (Savolainen and Vepsäläinen 1988, 1989; Savolainen et al. 1989; Punttila et al. 1991), *Iridomyrmex* (Fox et al. 1985; Andersen and Patel 1994) or *Oecophylla* (Andersen 1992) in natural communities, and *Solenopsis* (Camilo and Phillips 1990; Porter and Savignano 1990; Perfecto 1991) or *Linepi-*

thema humile (Ward 1987; Cole et al. 1992; Human and Gordon 1996) in disturbed communities, behave similarly by excluding other potential competitors from their territory and reducing the foraging success of subordinate species (Savolainen 1990, 1991; Vepsäläinen and Savolainen 1990; Andersen and Patel 1994; Perfecto 1994). This phenomenon of community structuring by dominant species appears to be a characteristic feature of the boreal zone (Savolainen and Vepsäläinen 1988, 1989; Savolainen et al 1989; Punttila et al. 1991, 1994) and tropical ant faunas (Samways 1981, 1983; Perfecto 1991; Morrison 1996; but see Davidson 1997, or Floren and Linsenmair 1997).

Recently, this prevalent view has moved to one giving more prominence to non-equilibrial and stochastic factors, such as physical disturbance and inconstancy in conditions (Begon el al. 1996). With linear hierarchies, high diversity may be maintained by predation or physical disturbances affecting the top dominant species differentially (Savolainen and Vepsäläinen 1989). If environmental conditions change so that each species is favored alternately within time periods clearly shorter than the colony life of the species, then these competing species could coexist indefinitely (Murray 1986). In Mediterranean communities, where environmental factors show important daily and seasonal variation, the limited thermal tolerance of dominant species compared with that of subordinates disrupts the expected transitive hierarchies, and allows a more substantial presence of the subordinate species in the ecosystem than might be expected from their relative abundance and fighting abilities (Cerdá et al. 1997). Under these competitive circumstances, subordinate species are expected to reduce the probability of interference with dominants by foraging at different times. The general idea is that there is a selection against simultaneous foraging with dominants because, within the range of overlapping activity periods, recurrent contact with competitors results in a reduction of foraging (Heatwole and Muir 1989; Vepsäläinen and Savolainen 1990). When hostile contacts are few, foraging success would be maximized with the result that subordinates would tend to forage at rather restricted times, even though their responses to weather conditions would permit a broader foraging time (Heatwole and Muir 1989). Nevertheless, temporal separations in foraging can also result from non-competitive causes such as physiological tolerance to physical conditions (Fellers 1989; Cerdá et al. 1998). In fact, many studies have found that the above-ground foraging activity of ants is related to soil temperature and is probably thermally regulated (Porter and Tschinkel 1987; Marsh 1988; Andersen 1992, Wehner et al. 1992).

In this paper we analyze the influence of these two contrasting mechanisms for community structuring – interference competition by dominant species and tolerance to temperature – on the foraging of subordinate species in Mediterranean ant communities. Our hypothesis is that the foraging of subordinate species in these ant communities is more affected by temperature than by competition of dominants, in contrast to the case in boreal and tropical communities. Our way of determining the role of dominant ants on the foraging of subordinates has been to choose different portions of a large area with similar ant composition, ground cover and vegetation structure (see Materials and methods), but different relative abundances of dominant ants. In this natural scenario, we have evaluated the effect of dominants on the foraging of subordinates by measuring different variables of foraging populations of subordinate species which may be regulated by competition: forager abundance (Andersen 1988; Savolainen 1990), foraging efficiency (Vepsäläinen and Savolainen 1990; Savolainen 1991; Andersen 1992; Andersen and Patel 1994), and foraging times (Hölldobler 1986; Savolainen and Vepsäläinen 1988; Vepsäläinen and Savolainen 1990). We have also tested the effect of temperature, which may be used as a "synthetic" variable to define climatic suitability for ant activity (Hölldobler and Wilson 1990; Cros et al. 1997), on these variables by analyzing natural shifts in resource use as thermal conditions temporarily change both daily and seasonally.

Materials and methods

Study site

This study was conducted in Llanos de Palomares, Sierra Sur de Jaén (Jaén province, southeastern Spain) in 1996. The climate is of a Mediterranean type. The mean annual temperature within the study area is 14.3°C. July and August are the driest months, and rainfall is concentrated in the winter half of the year (November through April). The area is an open grassland, with a clear understory of scattered herbs less than 5 cm tall surrounded by large portions of bare soil. Outside the study zone, only scattered holm oaks (*Quercus ilex*) were found in the overstory layer. The total area of the site was 4 ha. The ant fauna of this site was composed of 12 species, although only 9 were relatively abundant and are considered in this study. They represented 99.9% of the total ant fauna collected in traps, and 99.7% at baits.

Sampling

Based on previous sampling, we identified three different levels of density of dominant ants: low, medium, and high (hereafter, LDD, MDD, and HDD, respectively). For each of these levels, four different plots (= replicates) of 200 m^2 each were established. There were no differences among LDD, MDD, and HDD plots in aspect, vegetation cover and height, or ground temperature (ANOVA, $P > 0.05$ in all cases). Plots only differed in the abundance of dominant ants (for the identification of dominant ants, see the Results. Field observations were carried out in two different sampling periods: mid-July (summer) and early October (autumn). In each period, diel observations were made during 4 days, separated by a rest time of 1 day after each observation day.

Pitfall traps provide a good estimate of the relative abundance of ant species foraging on the ground (Romero and Jaffe 1989; Olson 1991; Klimetzek and Pelz 1992; but see Marsh 1984) and were used to measure forager abundance. Two series of three traps (with 5 m spacing between two different traps and between series) were established in the center of each plot. Pitfall traps were 6 cm-diameter, 7 cm-deep plastic vials partially filled with water, 70% ethanol and soap. The contents of pitfall traps were emptied daily, and analyzed in the laboratory.

Food exploitation was analyzed with baits, which have been widely used in studies of ant communities (Fellers 1987; Savolainen and Vepsäläinen 1988, 1989; Morrison 1996; Cerdá et al. 1997). In each plot, ten baits were placed in three series of four, three and three baits each (with 5 m spacing between two adjacent baits and between series) on the same sampling days as pitfall traps to make their results directly comparable. Baits were plastic discs with different large-food rewards (honey, bacon, cheese, and biscuit) that were attractive to ants and could not be transported in one piece to the nest by foragers. Each hour, the number of ants of each species feeding at each bait was recorded. Following Cerdá et al. (1997), three different types of interspecific interactions were recorded at baits: (1) expulsion of one species by another; (2) escape of one species from the bait caused by the attack of another; (3) coexistence between workers of different species. Together with the hourly measurements of activity at baits, ground surface temperatures in the sun and in the shade were measured with a digital thermometer.

Data analysis

Dominance of species at food resources was analyzed by calculating the dominance index, which was the percentage of times that a species is dominant in all of its expulsion and escape encounters (Fellers 1987; Cerdá et al. 1997). A transitive hierarchy results when all species of higher rank outcompete all species of lower rank (Karlson and Jackson 1981). To measure the transitivity of the hierarchy obtained, dominance relationships between pairs of species were represented in a symmetrical matrix. This matrix was optimally sorted by ranking each species according to the number of species it dominated at baits. The number of zeros that remained in the upper right of the outcome matrix was used as a measure of transitivity (Gilpin et al. 1986).

Forager abundance for each sampling day and plot was estimated by pooling together the number of ants caught in all pitfall traps. Similarly, the total number of baits occupied by each species during each sampling day in each plot was used as a measure of its food exploitation intensity. Diversity of ant species in traps and at baits was calculated using the Shannon index, $H = -\Sigma(p_i \cdot \ln p_i)$, where p_i is the proportion of workers in traps or baits occupied by species i.

A measure of the foraging efficiency of each species was calculated from the abundance of each species at baits and in pitfall traps, following Baroni Urbani and Aktaç (1981). The a priori probability of food exploitation (PFE) is a measure of the specific density of foragers on the ground, which is defined as:

$$\mathrm{PFE} = \mathrm{NF}_i / \sum \mathrm{NF}_i$$

where NF_i is the number of foragers of species i in pitfall traps. The incidence of each species on baits (IB) is the proportion of baits exploited by each species:

$$\mathrm{IB} = \mathrm{B}_i / \sum \mathrm{B}_i$$

where B_i is the number of baits exploited by species i. The foraging efficiency of each species (FE) measured its efficiency incidence on baits by correcting IB relative to the abundance of workers in pitfall traps (PFE). To normalize this quantitiy between 0 and 1, FE is defined as:

$$\mathrm{FE} = 1 - e^{-(\mathrm{IB}/\mathrm{PFE})}$$

Two different measures of daily temperature were used: maximum daily temperature and mean daily temperature (the average of the hourly temperatures registered in each 24-h sampling). The relationship between temperature and bait exploitation of each ant species was established by dividing the whole range of temperatures registered in the field into two °C classes. For each species, we pooled the data over all sampling days and calculated the mean number of baits occupied in each temperature class.

Regression and ANOVA were used to test the effect of temperature and abundance of dominants on four variables of the subordinate species: forager abundance at pitfall traps, number of baits occupied per day, mean number of workers per bait, and FE. The regression of temperature and each of these variables was calculated for the four most abundant subordinate species in the area (*Aphaenogaster senilis*, *Messor barbarus*, *Cataglyphis velox*. and *C. rosenhaueri*, see Table 1). Different analyses were performed with maximum temperature and mean daily temperature as regressor variable.

The role of the abundance of dominants in the foraging of subordinates was tested by repeated-measures ANOVA tests. The density of dominants (low, medium, or high) was the independent variable, while the repeated measures were the four sampling days in each period. In these analyses, the residuals of the regressions of the different variables against temperature were employed instead of the original values to remove the effect of temperature. Inspection of residuals was carried out to check for normality and homoscedasticity. Data of forager abundance at pitfall traps and number of baits occupied per day were normalized by $\ln(x+1)$ transformation. No transformation was needed for mean number of workers per bait and FE. When multiple statistical tests were conducted on the same data set or on data used to discuss a common hypothesis, the sequential Bonferroni method was employed to control the group-wide type I error rate (Rice 1989). Values in this paper are given as mean ± SE. All analyses were carried out using the SuperAnova package (Abacus Concepts 1989).

Results

Species composition and dominance hierarchy

From the nine ant species considered in this study, seven were recorded in the LDD plots (see next paragraph for the identification of dominant species), eight in the MDD plots, and nine in the HDD plots. The most abundant species (two sampling periods pooled) were *M. barbarus* (67.0%), *Tapinoma nigerrimum* (11.8%), and *C. velox* (10.3%) in LDD plots, the same three species and *A. senilis* in MDD plots (*M. barbarus* 49.6%; *T. nigerrimum* 24.6%; *A. senilis* 10.5%, and *C. velox* 9.8%), and *Pheidole pallidula* (27.3%), *T. nigerrimum* (25.7%), *M. barbarus* (19.9%), and *Tetramorium semilaeve* (11.1%) in HDD plots. Diversity in traps was $H = 1.77$ in HDD plots, $H = 1.37$ in MDD plots, and $H = 1.12$ in LDD plots.

The competitive status of the most abundant ant species in the area was determined by analyzing interspecific interactions at baits. Since there were no apparent differences among plots in the result of competitive interactions at baits, and to increase the size of the data set, interspecific encounters in all plots were pooled together. Differences in the proportion of competitive interactions among plots with different abundance of dominants were significant ($\chi^2 = 75.7$, $P < 0.0001$): aggressive interactions were more frequent in HDD plots (68.1% of aggressive interactions in all interspecific encounters at baits) than in LDD and MDD plots (28.4 and 22.2%, respectively). To determine the dominance hierarchy of the whole ant community and the species-species pair relationships, dominance relationships among the ant species found in the area are summarized in Tables 1 and 2. The three species (*T. semilaeve*, *P. pallidula*, and *T. nigerrimum*) with a dominance index greater than 50% and significantly different than that of the other species (see Table 1) were included in the group of dominants (hereafter, dominant species), while the remaining species were considered subordinates. Dominant species represented 13.4% of ants collected in traps in LDD plots, 27.3% in MDD plots, and 64.1% in HDD plots. There was a very clear transitive dominance hierarchy in this community (4% intransitivity): most species of higher rank (ranked according to the dominance index, i.e. higher dominance index) outcompeted species of lower rank (i.e., lower dominance index) at baits (Table 2). This dominance hierarchy took the form of both aggression and avoidance, in which lower-ranked species quickly left or were driven away from baits upon encountering a higher-ranked species.

Relationship between temperature and foraging of subordinate species

Since the maximum daily temperature and the mean daily temperature were highly correlated ($r^2=0.80$ in summer and $r^2=0.79$ in autumn, $P=0.0001$ in both seasons) and produced similar results, only analyses with the maximum daily temperature are shown hereafter. The relationships between maximum daily temperature and the variables describing the foraging of subordinate species were significant for all variables, except for the foraging efficiency (Table 3). For the remaining variables, many of the correlations with temperature calculated for the different species and in the two periods were significant (13 out of 18, 72%): forager abundance of *A. senilis* in the two sampling periods, and of *M. barbarus* in summer were significantly correlated to maximum daily temperature; the total number of baits exploited by all subordinate species in both periods was also related to temperature, while temperature also affected the total number of workers per bait for the four species in the summer period.

Effect of density of dominants on foraging of subordinates

Table 4 summarizes the effects of the density of dominants on the four variables used to describe the foraging of subordinate species, once the effect of temperature has been removed. In most cases (21 out of 24, 87.5%), there was no effect of the density of dominants on the foraging of subordinates, especially for two variables, the number of workers per bait and the foraging efficiency, which did not show differences among areas with different density of dominants for any species or period. For the other two variables, the only significant cases (i.e., indicative of competition) were those of *C. velox* and *M. barbarus* in summer for the number of baits occupied per day, and that of *C. velox* in summer for the number of foragers at pitfall traps. In these three cases, subordinate species were less represented at baits or in traps in the HDD plots than in the MDD or the LDD plots.

Since interference competition from dominant species may also regulate the timing of activity by subordinates, daily activity of subordinates in plots with different densities of dominants was plotted. Results shown in Fig. 1 indicate that mean activity rhythms of subordinates in the summer period were very similar in LDD, MDD, and HDD plots (*A. senilis*: $\chi^2=9.5$, $P=0.98$; *C. velox*: $\chi^2=10.1$, $P=0.98$; *C. rosenhaueri*: $\chi^2=9.1$, $P=0.96$; *M. barbarus*: $\chi^2=21.1$, $P=0.98$). In autumn, activity rhythms of *A. senilis* and *M. barbarus* shifted to unimodal and diurnal, but were still similar in the three types of plots (*A. senilis*: $\chi^2=21.2$, $P=0.17$; *M. barbarus*: $\chi^2=18.4$, $P=0.68$).

These similarities between areas with different abundance of subordinates were also evident in the curves of temperature versus foraging activity (Fig. 2). The maximal activity temperature was the same in the three types of plots for *M. barbarus* (18°C), *C. velox* (42°C) and *C. rosenhaueri* (42°C), and varied slightly in *A. senilis* (34°C in LDD and MDD plots, and 36°C in HDD plots). Subordinate species also started and ceased external activity at the same temperature in all types of plots, except for *C. velox*, which started foraging activity at 32°C in HDD plots compared to 28°C in LDD and MDD plots.

Table 1 Dominance hierarchy of ant species at baits: dominance relationships and interspecific encounters. Species are ranked according to their dominance index. Species sharing the same *superscript* do not differ significantly in the relative frequency of expulsion vs escape interactions (χ^2-test, significant at $\alpha=0.05$ when the sequential Bonferroni method is employed) (*N* number of interactions observed)

Species	Interspecific encounters				Dominance index	
	N	Expulsion (%)	Coexistence (%)	Escape (%)	*N*	%
Tetramorium semilaeve	28	89.3	7.1	3.6	26	96.1^a
Pheidole pallidula	91	60.4	28.6	11.0	65	84.6^a
Tapinoma nigerrimum	157	27.4	53.5	19.1	73	52.9^b
Messor barbarus	106	22.7	37.7	39.6	64	37.5^c
Aphaenogaster senilis	221	12.7	65.6	21.7	76	36.8^c
Crematogaster sordidula	19	26.3	26.3	47.4	14	35.7^c
Camponotus cruentatus	33	6.1	75.8	18.1	8	25.0^c
Cataglyphis velox	308	3.6	83.8	12.6	50	22.0^c
Cataglyphis rosenhaueri	137	2.9	85.4	11.7	20	20.0^c

Table 2 Dominance hierarchy of ant species at baits: two-dimensional array of the outcome of bait interactions between pairs of species. A *1* in row *i* and column *j* indicates that the *i*th species excluded the *j*th species; a 0 indicates the opposite; a dash (–) indicates that there were not enough encounters to determine the outcome of the interaction

Species	*Tsem*	*Ppal*	*Tnig*	*Mbar*	*Asen*	*Csor*	*Ccru*	*Cvel*	*Cros*
T. semilaeve		1	1	1	1	1	–	–	–
P. pallidula	0		1	1	1	1	1	1	1
T. nigerrimum	0	0		1	1	1	1	1	–
M. barbarus	0	0	0		1	–	–	–	–
A. senilis	0	0	0	0		0	1	1	1
C. sordidula	0	0	0	–	1		–	–	–
C. cruentatus	–	0	0	–	0	–		1	1
C. velox	–	0	0	–	0	–	0		
C. rosenhaueri	–	0	–	–	0	–	0	0	

Table 3 Correlation coefficients between mean daily temperature and the four variables describing the foraging of subordinate species, in the two sampling periods. *C. velox* and *C. rosenhaueri* were almost absent in the autumn sampling and correlations have not been performed for them. Significant coefficients (at $\alpha = 0.05$ when the sequential Bonferroni method is employed) are indicated in *italics*

Variable	*M. barbarus*		*A. senilis*		*C. velox*	*C. rosenhaueri*
	Summer	Autumn	Summer	Autumn	Summer	Summer
Number of foragers in traps	*0.402*	0.292	*0.412*	*0.450*	0.187	0.227
Baits occupied/day	*0.566*	*0.549*	*0.639*	*0.435*	*0.507*	*0.419*
Number of workers/bait	*0.422*	0.130	*0.418*	0.149	*0.548*	*0.399*
Foraging efficiency	0.182	0.006	0.115	0.114	0.063	0.182

Table 4 *F*-values from repeated-measures ANOVA tests of effects of density of dominants (*DD*) as independent variable, and days (time, *T*) as repeated measures on the four variables describing the foraging of subordinate species in the two sampling periods. To remove the effect of temperature, the residuals of the regressions of the different variables against temperature have been used instead of the original variables. *C. velox* and *C. rosenhaueri* were almost absent in the autumn sampling and ANOVAs have not been performed for them. Data of forager abundance at pitfall traps and number of baits occupied per day were $\log(x+1)$ transformed. Significant coefficients (at $\alpha = 0.05$ when the sequential Bonferroni method is employed) are indicated in *italics*

Variable	Source of variation	*M. barbarus*		*A. senilis*		*C. velox*	*C. rosenhaueri*
		Summer	Autumn	Summer	Autumn	Summer	Summer
Number of foragers in traps	Density of dominants (DD)	0.06	0.04	1.51	0.49	*14.93*	0.07
	Time (T)	5.19	0.96	0.58	0.95	5.89	4.04
	DD × T	0.57	1.34	1.90	1.01	4.01	4.04
Baits occupied per day	Density of dominants (DD)	*20.85*	0.91	0.87	1.19	*65.47*	1.36
	Time (T)	4.41	3.08	0.58	4.03	5.35	0.90
	DD × T	0.41	3.10	1.54	1.32	2.44	2.16
Number of workers per bait	Density of dominants (DD)	0.52	0.25	11.48	5.32	5.89	2.84
	Time (T)	0.28	0.76	3.40	5.36	2.10	3.15
	DD × T	3.98	0.29	0.60	0.62	0.80	3.34
Foraging efficiency	Density of dominants (DD)	0.06	0.61	1.83	0.21	1.02	2.10
	Time (T)	1.83	1.04	7.52	0.24	0.97	0.46
	DD × T	1.57	1.14	2.23	1.17	1.17	0.73

Discussion

Species dominance has been defined as the appropriation of potential niche space of certain subordinate species by dominant species (McNaughton and Wolf 1970). If this is true, the presence of dominant species should reduce the foraging success of other species. In ants, this has been confirmed in many cases (Savolainen and Vepsäläinen 1989; Savolainen 1990; Andersen and Patel 1994; Perfecto 1994), and aggressive interactions with dominants have even contributed to the disappearance of certain species (Human and Gordon 1996). In the absence of dominant ants, subordinate species increase colony size (Savolainen 1990), produce more

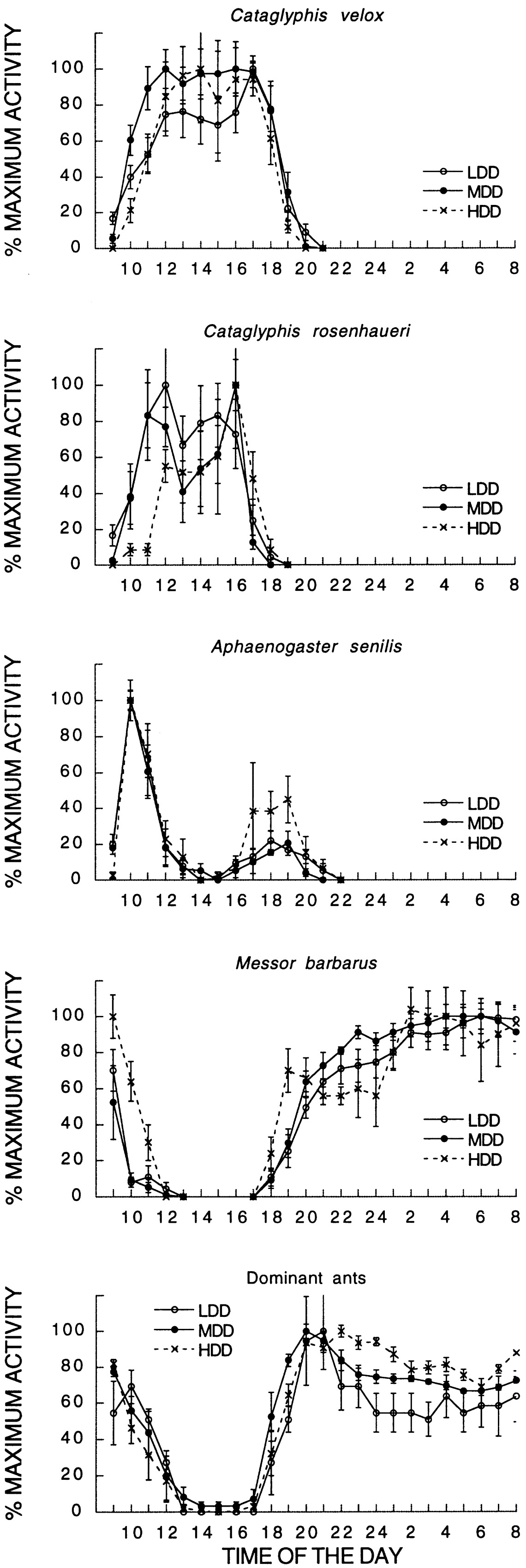

Fig. 1 Mean (±SE) foraging activity rhythms in summer of the four subordinate species and the three dominant species (*Tetramorium semilaeve*, *Pheidole pallidula*, and *Tapinoma nigerrimum*) pooled together in plots with low (*LDD*), medium (*MDD*) and high (*HDD*) density of dominants. Data have been standardized by defining the maximum hourly activity value for each level of dominant density as 100% of activity

worker and sexual offspring (Savolainen 1990), increase their presence at food resources (Vepsäläinen and Savolainen 1990; Andersen 1992; Andersen and Patel 1994), and expand their foraging times to more favorable periods of the day (Savolainen and Vepsäläinen 1988, 1989), even shifting them from nocturnal to diurnal or vice versa (Vepsäläinen and Savolainen 1990; Andersen and Patel 1994).

In the ant community studied here, there was a clear transitive dominance hierarchy, with dominant species outcompeting subordinate species when they encountered each other at food resources (Tables 1,2). However, the expected effects of the competition of dominants on subordinates were only detected in 12.5% of cases. Subordinate species present in plots differing in abundance of dominant ants rarely showed differences in the variables analyzed. This was true for species such as the two *Cataglyphis*, that did not overlap in their foraging times with dominants, but also for species that partly (such as *A. senilis*) or almost completely (such as *M. barbarus*) overlapped with dominants. A reduction in the abundance of dominants was not correlated to any increase in number of workers per bait or specific foraging efficiency of subordinate ants, and there were only two cases of significant differences in the number of baits occupied, and one in the number of ants in traps (Table 4). Moreover, if foraging times of subordinates are limited by the interference of dominants, they should forage across a broader time range, although always within their physiological limits, when dominants are absent. Nevertheless, the daily activity rhythms and the curves of temperature versus foraging activity of subordinate species were similar in plots with different densities of dominants, indicating no effect of dominants on the foraging times of subordinates.

Instead, temperature had a stronger effect on the foraging of subordinate species. Thus, forager abundance of *A. senilis* in the two sampling periods, and of *M. barbarus* in summer was significantly related to maximum daily temperature; the total number of baits exploited by all subordinate species in both periods was also related to temperature, while temperature also affected the total number of workers per bait for the four species in the summer period (Table 3). Daily and seasonal foraging shifts of subordinate species were best interpreted as responses to temperature. On cool days, subordinates started external activity later in the morning, showed a shorter drop at midday, and returned to the nest earlier in the afternoon, whereas on very hot days, subordinates started foraging earlier, showed a

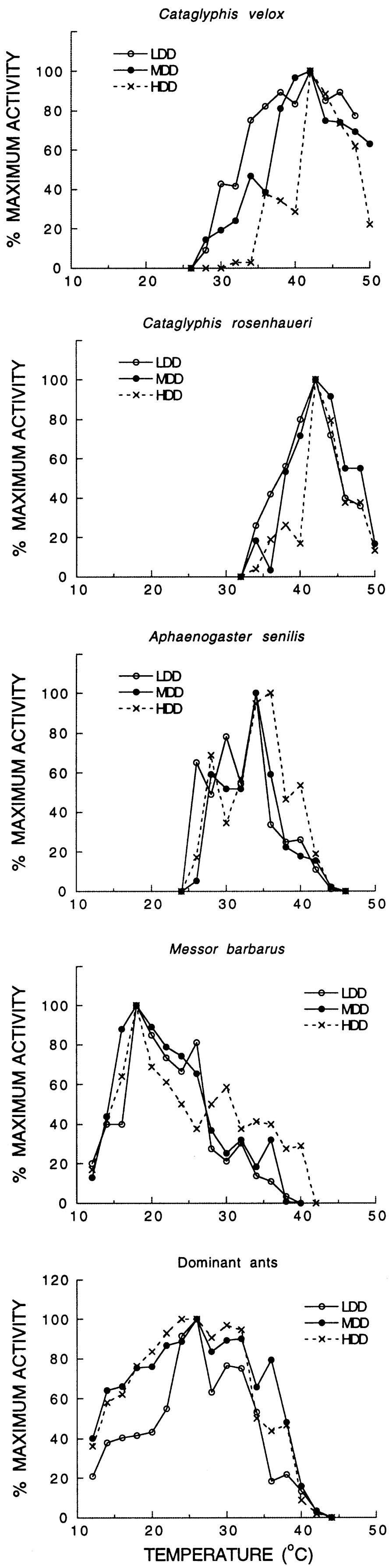

Fig. 2 Curves of temperature versus foraging activity of the four subordinate species and the three dominant species (*Tetramorium semilaeve*, *Pheidole pallidula*, and *Tapinoma nigerrimum*) pooled together in plots with low (*LDD*), medium (*MDD*) and high (*HDD*) density of dominants. Each point represents the mean activity value of all cases with the same temperature (in 2°C classes). Data have been standardized by defining the maximum mean activity value for each level of dominant density as 100% of activity

larger midday drop, and returned later to the nest in the afternoon (data not shown). Many species showed greater activity in summer than in autumn; several subordinate species also shifted summer activity curves from bimodal to unimodal (e.g., *A. senilis*) or from nocturnal to diurnal (e.g., *M. barbarus*) in autumn, when diurnal temperatures were about 15–20°C lower than in summer; finally, the two most thermophilic ants (i.e., the two *Cataglyphis* species) were almost absent in the autumn period, when temperatures were too low for them during most of the day, even though many baits remained unoccupied at that time.

These results suggest that temperature rather than interspecific competition primarily determines the temporal activity patterns found in ant communities of open Mediterranean habitats (see also Cerdá et al. 1997; Cros et al. 1997). Temporal separation of activity rhythms has been considered advantageous when competition involves intense interference interactions, because subordinate species might be expected to reduce the probability of exclusion by dominants by foraging at different times, mainly at night and/or at low temperatures (Savolainen and Vepsäläinen 1989; Paulson and Akre 1991). Nevertheless, in the communities studied, this mutual exclusion, when observed, appears to be merely the result of different circadian activities and physiological traits. Although it is common to find no marked differences between dominants and subordinates in their response to temperature (Vepsäläinen and Savolainen 1990; Andersen 1992), Cerdá et al. (1997, 1998) record for open Mediterranean habitats that dominant ants are restricted largely by environmental conditions, whereas subordinates are active over a wider range of temperatures. These differences in the response to temperature, together with the high environmental fluctuations observed (Cros et al. 1997), might explain the reduced effect of interspecific competition in structuring these ant communities. We cannot rule out the possibility that interference competition takes place in certain areas or periods of the day or the year when there are substantial differences in temperature. These differences determine differences in the abundance of dominant species, which in turn regulate the abundance and foraging success of subordinate species. Nevertheless, this pattern occurs on such a small spatial or temporal scale that it is probably not effective in structuring whole communities (Cros et al. 1997).

This study shows that interference interactions led to a competitive hierarchy of ant species, but there was no demonstration of true or depressive competition (sensu Mac Nally 1983) of foraging of subordinate ants by dominants, although food resources were presumably limiting in these habitats (baits were occupied by ants during most of the day, at least in the summer period, and interference interactions were common when ants encountered each other at baits). In these communities living in severe, variable and predictable environments (sensu Slobodkin and Sanders 1969, in Putman 1994), climatic axes appear to have a primary role in community structure, and resistance to physical factors reduces the occurrence of competition (Schoener 1986).

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