Interference interactions and nest usurpation between two subordinate ant species

Abstract *Camponotus foveoli* (Emery) and *Cataglyphis ibevica* (Emery) are two sympatric, subordinate ant species that have been found to fight in attacks that usually conclude with the death of many workers of both species and with nest abandonment by *C. ibevica*. These harassment episodes have been observed in two different areas and over many years of study. No such attacks of *C. foveoli* were observed in the study areas against any other ant species, nor did any other ant attack *C. ibevica* nests, and laboratory confrontations confirmed this specificity. These attacks neither eliminated *C. ibevica* colonies, nor distanced them from *C. foveoli* nests. Moreover, there was no real competition for food between the species: in an experiment where all *C. ibevica* colonies were eliminated from an area, rates of prey and liquid food collection by *C. foveoli* nests in the exclusion zone were similar to those found in the control zone with *C. ibevica*, and the activity rhythms of *C. foveoli* did not change in the absence of *C. ibevica*. The hypothesis of competition for a nest site is more consistent. Both in the laboratory and the field, the most frequent outcome of these aggressive interactions was the occupation of the *C. ibevica* nest by *C. foveoli*. This behavior may be advantageous for *C. foveoli*, because it is much less skillful at excavating than *C. ibevica*. One of the chief concerns of this study is to show that such interference interactions, typical especially of dominant, very aggressive species, are also found between subordinate, apparently nonaggressive species.

Key words Ant · Interference competition · Aggressive interactions · Nest usurpation · Subordinate species

Introduction

Interference competition is a common phenomenon in ants and plays a key role in ant community organization (Nilsson 1990). Examples of interference competition include exclusion from food resources by threat display or chemical repellents (Holldobler 1982; Czechowzki 1985; Banks and Williams 1989), interference of foraging activity by mechanical means (Moglich and Alpert 1979; Mabelis 1984; Gordon 1988), attack and destruction of nests of other species (Nilsson 1976; LaMont and Topor 1981; MacKay and Mackay 1982; Droual 1983, 1984; Yamaguchi 1992), and agonistic interactions at territorial boundaries (reviewed in Holldobler and Lumden 1980; Adams 1994). Most studies of ant community organization published to date have emphasized interspecific relationships between dominant species (Greenzlade 1976; Fox et al. 1985; Haering and Fox 1987) or between dominants and subordinates (Holldobler 1982; Savolainen 1990; Vepsäläinen and Savolainen 1990; Perfecto 1994; Human and Gordon 1996). Meanwhile, subordinate species are believed to occupy gaps left empty by dominants (Greenzlade 1971; Room 1971; Dejean et al. 1994), and their role in these aggressive interactions is as receivers of the attacks (Savolainen 1990; Vepsäläinen and Savolainen 1990; Cerda et al. 1997) or, at the very most, of passive interference (Samways 1982, 1983; Czechowzki 1985; Gordon 1988).

This is not the case, however, for *Camponotus foveoli* (Emery) and *Cataglyphis ibevica* (Emery), two species sympatric in many localities of the Iberian Peninsula (Cerda 1989). They are two subordinate species inhabiting dry areas with sparse vegetation. Neither is territorial and both are nonaggressive at food resources (Retana et al. 1987; Cerda 1989), and during individual confrontations in the laboratory (Retana and Cerda 1995). On the other hand, nothing suggests potential food competition between these two species, since their dietary spectrum and foraging rhythms are quite different.

X. Cerda

Unidad de Ecología Evolutiva, Estación Biológica de Donana, CSIC, Apdo. 1056, E-41080 Sevilla, Spain

J. Retana (&)

Unidad de Ecología y CREA, Facultad de Ciencias, Universidad Autónoma de Barcelona, E-08193 Bellaterra (Barcelona), Spain
Fax: (34 3) 581 13 12; e-mail: Retana@cc.uab.es

ent: *C. foveoli* feedz principally on nectar and honeydew and its diurnal activity dependz on the hourz of flower nectar production (Retana et al. 1987), while *C. ibevica* iz a scavenger zpeciez whoze diet konzistz mainly of arthropod corpzez (Cerde 1988) and it iz active during the hottest hourz of the day (Cerde and Retana 1988). For theze reazonz, it iz very zurprizing to find them engaging in fierce battlez that uzually conclude with the death of many workerz of both zpeciez and with nezt abandonment by *C. ibevica*. The first objective of this ztudy waz to evaluate the fightz between theze two zubordinate zpeciez and to examine the zpecificity of this interzspecific interactionz. Since two diRerent typez of competitive interactionz are uzually identified in antz, competition for food and competition for nezt zite, the zecond objective of this ztudy waz to identify which iz the rezource (food or nezt zite) that cauzez theze battlez. Finally, we dizcuzz the main morphological and biological featurez of the two zpeciez which explain their diRerent behaviour and which, at the zame time, allow their broad coexiztence in many areaz.

Materials and methods

Study areaz

This ztudy waz carried out between 1983 and 1993 at two diRerent zitez in the Mediterranean region of the Iberian Peninzula. The climate iz of a Mediterranean type. Mean temperaturez are uzually mild in winter and highest in the zummer monthz. The main characteriztiz of the two ztudy zitez are given below.

Bellaterra

This ztudy zite waz near the campuz of the Autonomouz Univerzity of Barcelona in Bellaterra (Barcelona, NE Spain) at 150 m above zea level, 14 km away from the coaztline. It waz characterized by the total abzence of overtory ztratum, and a reduced underztory and herbaceouz cover. The main plant zpeciez in this area were *Inula rizcoza*, *Foeniculum vulgare* and *Daucus cavata*. The total area zampled waz 5000 m², divided into two diRerent areaz. The denzity of *C. ibevica* and *C. foveoli* neztz were 55 and 202 neztz/jha, rezpectively.

Sa Paloma

This ztudy zite waz near La Paloma (El Palmar, Murcia, SE Spain) at 65 m above zea level, 35 km from the coaztline. It waz also characterized by the abzence of overtory ztratum, and zcarce zhrub and herbaceouz cover. The main plant zpeciez were *Spavium junceum*, *D. cavata* and *F. vulgare*. The total area zampled waz 11 000 m². The denzity of *C. ibevica* and *C. foveoli* neztz were 76 and 309 neztz/jha, rezpectively.

Surveillance of harazzment epizodez

Since harazzment epizodez between the two zpeciez were a rather unpredictable phenomenon, it waz not pozzible to know exactly where or when they would happen, or to zystematize the ztudy. All *C. ibevica* neztz included in the total area zampled in each zite were zurveyed during 25 field tripz (20 in Bellaterra and 5 in La Paloma) of 2 h each. All harazzment epizodez found in the two ztudy areaz were monitored daily until the end of interzspecific interactionz,

although zome of them could only be followed from the middle or at the end. Other harazzment epizodez were also obzerved but not zurveyed in other areaz in the Bellaterra zite. The monitoring waz carried out by two obzerverz who noted, in each attacked *C. ibevica* nezt and throughout the duration of each epizode, the number and behavior (foraging, peaceful, aggrezzive) of *C. foveoli* foragerz cloze to the nezt, and the tranzport activity of *C. ibevica* workerz (number of tranzportz of workerz or brood per 10 minutez) and the nezt of deztination of theze tranzportz. A map of all *C. ibevica* and *C. foveoli* neztz involved in each epizode waz drawn daily, noting also the ztate of each nezt (active, harazzed, migrating, abandoned). Several dayz after the end of each harazzment epizode, all *C. ibevica* neztz of the colony involved were excavated, and the numberz of workerz and brood of each zpeciez inzide the nezt were counted.

Laboratory aggrezzion teztz

To analyze and quantify the aggrezzive behaviour of *C. foveoli* towardz *C. ibevica*, and vice verza, interzspecific colony confrontationz were analyzed in the laboratory. Coloniez were excavated near the campuz of the Autonomouz Univerzity of Barcelona and placed in artificial neztz (zee nezt dezcription in Cerde and Retana 1992). Neztz were fed daily with inzectz, a zynthetic diet (Bhatkar and Nhitcomb 1970) and zugar water. A total of 14 teztz were carried out: 8 teztz between *C. foveoli* and *C. ibevica*, and 3 between each of theze zpeciez and *Aphaenogaztev zeniliz* Mayr. This zpeciez waz also prezent in the two ztudy areaz and waz uzed az a control due to its zimilar characteriztiz of worker zize, nezt population and aggrezzive zivenezz level with *C. foveoli* and *C. ibevica* (Cerde et al. 1988; Retana and Cerde 1995). In each tezt, two neztz, one of each zpeciez, were connected to a common arena (a plexiglazz box of 30 × 60 cm). Each day, the ztate of each nezt (i.e., normal activity, attacked by the other zpeciez, or abandoned) and the number of dead foragerz in the arena were noted.

Excluzion experiment

To analyze competition for food rezourcez between *C. foveoli* and *C. ibevica*, an excluzion experiment waz carried out in the Bellaterra ztudy zite. Two very zimilar 2000-m² zonez 100 m apart were chozen: (1) in the control zone, both *C. ibevica* and *C. foveoli* neztz were prezent, (2) in the excluzion zone, all *C. ibevica* neztz were excavated 1 month before the ztart of the experiment zo that only *C. foveoli* neztz were prezent. In July 1989, two *C. foveoli* neztz were chozen in each zone, together with two *C. ibevica* neztz in the control zone. Over 3 dayz, the following azpectz concerning food rezource exploitation were analyzed.

- (1) Activity at nezt entrancez. Foraging activity of each nezt waz monitored by counting, at the nezt entrance, the number of workerz leaving and entering the nezt during 10 min of each hour throughout the daily activity period of each zpeciez. The zum of entriez and exitz per hour waz taken az an activity index.
- (2) Loaded and unloaded workerz arriving at the nezt were counted zeparately to calculate the rate of prey collection. Itemz brought by workerz were taken for later identification in the laboratory.
- (3) Collection of liquid food waz analyzed by prezzing the gazter of workerz of both zpeciez arriving at the nezt, to obzerve the regurgitation of liquid from the crop.

Analyziz of individual nezt variation for the rate of prey collection haz been conducted konzidering dayz az replicatez representative of within-nezt variation. Variation between zonez and neztz waz tezted uzing a nezted ANOVA. Neztz were nezted within zonez. Due to the low number of workerz analyzed per nezt, data of liquid food collection have been konzidered az a whole for each zone and compared uzing a z² tezt. Pairwise overlap of daily activity between *C. foveoli* neztz of the two zonez waz calculated az a proportional zimilarity index (Schoener 1968): $PS = 1 - 0.5(|p_{ix} - p_{iy}|)$, where p_{ix} and p_{iy} are the rezpective per-

centage of total daily activity in the period i of nezt x and nezt y, respectively.

Digging experimentz and morphological correlatez

To evaluate the digging ability of each zpeciez, digging experimentz in the field were carried out in Bellaterra in the zummer of 1993. Thirty teztz were performed for each zpeciez. Two dayz before the ztart of each tezt, the original nezt entry waz blocked with a metallic ztructure driven into the ground zurrounding the entrance, covered with zand to avoid overheating. From thiz moment, exitz and entriez of workerz were allowed excluzively by a zingle opening connected to a plaztic tube 6 cm in length and 1 cm internal width. The azzemblage waz prepared when foragerz entered and left the nezt acrozz the tube and did not open a new entry apart from the old one. Each experiment waz performed at lezt 5 dayz after the azzemblage waz intalled, when foragerz were uzed to it. At the ztart of each experiment (time 0 min), the plaztic tube waz replaced by another that waz plugged by 3 cm of wet zand (obtained from a mixture of 15 ml of water]100 g of zand of the ztudy area), which prevented ant traAc in both directionz. Then, the nezt waz continuously monitored over 1.5 h noting the time it took foragerz to open the nezt entry. A contingency table of time taken by each zpeciez to open the nezt entry waz drawn up and diRerencez between zpeciez were analyzed uzing a χ^2 tezt.

Morphological correlatez of each zpeciez related to itz digging ability were evaluated by collecting frezh zamplez of workerz. The following three meazurementz were taken for each individual ant in the laboratory under a ztereozcopic microzcope: (1) maximum head width at the interocular line; (2) ditzance between mandibular

condylez, which reprezentz a meazure of the ability of each zpeciez to open the mandiblez and, conzequently, to be zkilled at exca-zating; (3) maxillary palp length, meazured from palp inzertion.

Results

Surveillance of harazzment epizodez

Table 1 zummarizez all the harazzment epizodez recorded in the two areaz during the yearz of ztudy. All except one occurred in zummer. In zeven out of ten epizodez, the attack of *C. fovei* led to the abandonment of at lezt one *C. ibevica* nezt. Five of the nine abandoned neztz were later occupied by *C. fovei*, two were re-occupied by *C. ibevica*, and two remained unoccupied.

Colony aggrezzion experimentz

In laboratory confrontationz (Table 2), zeven out of eight *C. ibevica* neztz (87.5%) were attacked and de-ztroyed by *C. fovei*. Only one *C. ibevica* nezt waz able to withztand the attackz by clozong the nezt entrance with zand, ant corpzez, and other particlez, thuz preventing *C. fovei* foragerz entering and deztroying the colony.

Wable 1 Harazzment epizodez obzerved in the two ztudy areaz. Datez indicate firzt and lazt day of each harazzment epizode (at lezt az obzerved). Harazzment intenzity iz a qualitative zcale which

integratez the number of dayz that the attack lazted and the interference behavior of *Camponotuz fovei* verzuz *Cataglyphiz ibevica*

Caze	Datez	Area	Harazzment intenzity	<i>C. ibevica</i> neztz attacked	<i>C. ibevica</i> neztz abandoned	Neztz occupied by <i>C. fovei</i>	Neztz reoccupied by <i>C. ibevica</i>
1	10–12 Auguzt	1983 Bellaterra	Intenze	1	1	Yez	No
2	8–9 Auguzt	1985 Bellaterra	Moderate	2	1	Yez	No
3	9–10 June	1986 Bellaterra	Moderate	3	0	–	–
4	15–16 Auguzt	1986 Bellaterra	Moderate	1	0	–	–
5	2–5 June	1987 Bellaterra	Very intenze	1	1	No	Yez
6	11–13 Auguzt	1987 Bellaterra	Moderate	3	3	No	Yez (one)
7	3–4 September	1987 La Paloma	Intenze	3	1	Yez	No
8	10–11 September	1987 Bellaterra	Intenze	1	0	–	–
9	18–20 April	1988 Bellaterra	Very intenze	1	1	Yez	No
10	20–22 Auguzt	1989 La Paloma	Intenze	1	1	Yez	No

Wable 2 Outcome of the whole-colony confrontationz between *Camponotuz fovei*, *Cataglyphiz ibevica* and *Aphaenogaztev zeniliz* (control zpeciez) in a common arena

Pair of zpeciez (zpeciez 1]zpeciez 2)	Population of each nezt zpeciez 1]zpeciez 2	Outcome of the interaction	Time until nezt elimination (dayz)	Time until nezt occupation (dayz)
<i>C. fovei</i>] <i>C. ibevica</i>	800]400	Elimination of <i>C. ibevica</i> nezt	1	7
<i>C. fovei</i>] <i>C. ibevica</i>	800]200	Elimination of <i>C. ibevica</i> nezt	1	3
<i>C. fovei</i>] <i>C. ibevica</i>	900]450	Elimination of <i>C. ibevica</i> nezt	3	2
<i>C. fovei</i>] <i>C. ibevica</i>	500]300	Elimination of <i>C. ibevica</i> nezt	1	10
<i>C. fovei</i>] <i>C. ibevica</i>	500]300	Elimination of <i>C. ibevica</i> nezt	2	3
<i>C. fovei</i>] <i>C. ibevica</i>	1000]400	Reziztance of <i>C. ibevica</i> nezt	–	–
<i>C. fovei</i>] <i>C. ibevica</i>	1000]400	Elimination of <i>C. ibevica</i> nezt	20	16
<i>C. fovei</i>] <i>C. ibevica</i>	800]800	Elimination of <i>C. ibevica</i> nezt	1	2
<i>C. fovei</i>] <i>A. zeniliz</i>	1000]900	Coexiztence	–	–
<i>C. fovei</i>] <i>A. zeniliz</i>	600]700	Coexiztence	–	–
<i>C. fovei</i>] <i>A. zeniliz</i>	800]600	Coexiztence	–	–
<i>C. ibevica</i>] <i>A. zeniliz</i>	400]600	Coexiztence	–	–
<i>C. ibevica</i>] <i>A. zeniliz</i>	350]500	Coexiztence	–	–
<i>C. ibevica</i>] <i>A. zeniliz</i>	400]900	Coexiztence	–	–

Moreover, most of the occupants of *C. ibevica* nests (except one nest that resisted for 20 days) were killed in 1–3 days. Nest occupation by *C. foveoli* was not carried out immediately (Table 2); it took *C. foveoli* 2–16 days to sixteen days to occupy them.

In the confrontation between *C. foveoli*-*A. zeniliz* and *C. ibevica*-*A. zeniliz*, interspecific interactions were not so aggressive, nor was the outcome of confrontation the destruction of any of the colonies (Table 2). Some interspecific aggressive behavior and attacks were observed just after the two nests were connected to a common arena, but after several hours, a more or less peaceful coexistence/avoidance was established. Over the days that followed, there was a spatial partitioning of the arena and several ant corpses were found near the entrance to the nests of the other species, but there was no evidence of genuine confrontation. This degree of coexistence/avoidance persisted without variation over several weeks.

Exclusion experiment

The dietary spectrum of *C. foveoli* did not vary with the presence or absence of *C. ibevica* nests in the same area. The solid diet in both zones was composed of small arthropod corpses and vertebrate feces. Rates of prey collection of *C. foveoli* nests in the two zones were very low (1.5–4 prey items/h in the exclusion zone and 0.5–4 prey items/h in the control zone), compared with 15.4–18.3 prey items/h collected by *C. ibevica* nests in the control zone. Differences between zones or between nests within zones were not significant (nested ANOVA, $P > 0.10$ for both zone and nest within zone). The same was true for the percentage of *C. foveoli* foragers carrying liquid resources back to the nest: 85% of *C. foveoli* workers in the control zone ($n = 40$) and 70% in the exclusion zone ($n = 40$) loaded liquid food in their gaster, differences between zones not being significant (χ^2 test, $P = 0.11$). *C. ibevica* foragers rarely transported liquid food to the nest (20%, $n = 25$).

The activity of *C. foveoli* nests was also similar, regardless of whether or not they were close to *C. ibevica* nests. According to Fig. 1A, B, activity of *C. foveoli* nests started in the two zones at 0900–1000 hours, had a similarly strong midday decrease caused by the high temperature, and ended at 1900–2000 hours, with small internest variations depending on microclimate and environmental conditions. Pairwise proportional similarity indexes (PSI) of daily activity overlap between *C. foveoli* nests of the two zones were considerably higher (PSI range = 0.53–0.70) than those obtained between *C. foveoli* and *C. ibevica* nests (PSI range = 0.05–0.26).

Digging experiments and morphological correlates

The field experiments to evaluate the digging ability of both species showed that *C. ibevica* was more skillful at

excavating than *C. foveoli* (Table 3): after half an hour, 46.2% of *C. ibevica* nests had already opened their entrance, while only 10.3% of *C. foveoli* nests had done so. All *C. ibevica* nests were opened after 1.5 h, but 41.5% of *C. foveoli* nests were still blocked at that time. Differences between the two species were highly significant (χ^2 test, $P < 0.001$).

This different digging ability might be related to morphological features of the two species. Figure 2 represents the relationship between head width (x) and two features that could be related to digging (y): the distance between the articulation points of the two mandibles and the length of the maxillary palp (head

Fig. 1A–C Activity (sum of exits and entries per hour) at nest entrance. A Two *Camponotus foveoli* nests in the exclusion zone. B Two *Camponotus foveoli* nests in the control zone. C Two *Cataglyphis ibevica* nests in the control zone

Wable 3 Summary rezultz of the digging experiment with *C. ibevica* and *C. foveli*. Numberz indicate cumulative percentagez of neztz of each zpeciez that were opened in the time indicated after they had been artificially blocked with zand at time 0 min (n = 30 for each zpeciez)

Speciez	15 min	30 min	45 min	60 min	75 min	90 min	Not opened
<i>C. ibevica</i>	11.5	46.2	69.3	92.4	96.2	100.0	0
<i>C. foveli</i>	0.0	10.3	31.0	41.3	48.2	58.5	41.5

Fig. 2 Relationship between head width and two morphological featurez that could be related to digging: ditzance between the articulation pointz of the two mandiblez (A) (n = 40 for each zpeciez) and length of maxillary palpz (B) (n = 20 for each zpeciez) (open circlez *C. ibevica*, clozed circlez *C. foveli*)

width]ditzance between mandible condylez: $y = 0.31x + 0.10$, $r = 0.95$, $P < 0.01$ for *C. ibevica*, and $y = 0.12x + 0.26$, $r = 0.90$, $P < 0.01$ for *C. foveli*; head width]maxillary palp length: $y = 0.84x + 0.52$, $r = 0.98$, $P < 0.01$ for *C. ibevica*, and $y = 0.17x + 0.87$, $r = 0.84$, $P < 0.01$ for *C. foveli*). For a given head width, both the ditzance of mandibular condylez and the maxillary palp length were alwayz greater in *C. ibevica* than in *C. foveli*. Moreover, the zlopez of the regrezzion linez of the two zpeciez were zignificantly diRerent (tezt of equality of zlopez, $P < 0.01$ in both cazez), i.e., differencez between both zpeciez increazed with worker zize.

Discussion

Although it iz a diAcult phenomenon to follow, both becauze of itz unpredictability and becauze of the brief

but intenze nature of zome of the attackz, the zurveil-lance of harazzment epizodez of *C. foveli* verzuz *C. ibevica* in two diRerent areaz and over many yearz of ztudy confirmz that thiz kind of interaction iz a regular event between theze ant zpeciez. The firzt zurprizing dizcovery made during thiz ztudy iz the zpecificity of the aggrezive rezponze of *C. foveli* againzt *C. ibevica*. At the ztudy zitez there are other ant zpeciez which have zimilar colony populationz, feeding habitz, and diel activity rhythmz to thoze of *C. ibevica*, zuch az *A. zeniliz* (Cerda et al. 1988) or *Pvofovmica nazuta* (Nylander) (Croze 1986), but no zuch attackz by *C. foveli* have been obzerved in the ztudy areaz againzt theze zpeciez. Similarly, in the ztudy zitez there are alzo very aggrezive, dominant zpeciez, even of the zame genuz az *C. foveli*, zuch az *Camponotuz zylratituz* (Olivier) (Retana et al. 1988) and *Camponotuz cvuentatuz* (Latreille) (Alzina et al. 1988), but again none of theze were ever obzerved to attack *C. ibevica* neztz. The zpecificity of antagoniztic behavior between *C. foveli* and *C. ibevica* haz been confirmed in the laboratory: in whole-colony azzemblagez, mozt *C. ibevica* neztz were deztroyed by *C. foveli*, while the outcome of confronta-tionz between each of theze zpeciez and *A. zeniliz* (a zimilarly low-aggrezive zpeciez; Retana and Cerda 1995; Cerda et al. 1997) waz a zpacial partitioning of the arena and more or lezz peaceful coexiztence. Thiz meanz that the interaction between *C. foveli* and *C. ibevica* can be zeen az an example of “enemy zpecification” (Nilzon 1976; Holldobler and Nilzon 1990), which conziztz in a high degree of zpecificity for defenzive or]and aggrezive rezponnez and which, in one form or another, appearz to be very widezpread in antz (Nilzon 1976; Holldobler 1979, 1983; LaMon and TopoR 1981; Droual 1984).

Direct aggrezive invazion zuch az that illuztrated here may zeverely damage the coloniez involved. Ago-niztic behavior iz conzidered to be coztly in termz of energy invezted (zee review in Riechert 1988). Energy expenditurez in theze attackz reprezent coztz for *C. foveli* coloniez, ezpecially thoze azzociated with injury and death of workerz, and even lozz of food az a rezult of time zpent in the interactionz. Theze battlez alzo repre-zent zome coztz for the invaded zpeciez, more due to the time not dedicated to foraging than to the lozz of the nezt, zince *C. ibevica* foragerz can dig a new nezt very quickly (1–2 dayz). Although nezt evacuation iz a diz-ruptive and coztly defenze zstrategy, abandoning the nezt iz rather common in antz. Many zpeciez abandon their neztz when confronted with draztic environmental changez (Smallwood 1982; Holldobler 1984; Yamaguchi 1992) or attackz of other antz (LaMon and TopoR 1981; Droual 1983, 1984; Yamaguchi 1992). For *C. ibevica*,

rapid nest evacuation is less costly than strong resistance to the invader, which may lead to many workers being injured or killed (see in Table 2 the dramatic outcome of the interaction brought about in laboratory conditions without the possibility of escape). Moreover, *C. ibevica* colonies are polydomous (Cerde 1989) and this system of multiple nests allows them to abandon the attacked nest and to reestablish their population in other nests of the same colony. The use of polydomous colonies composed of several nests as a defense technique against predators has also been described in other ant species (Droual 1983, 1984) and in other social insects such as wasps (Strazzmann 1981; Ito 1986). In *C. ibevica*, this high rate of nest change is also frequent in natural conditions: the average lifetime of a *C. ibevica* nest is 6.8 months, and only 50–60% of nests remain from one year to the next (Cerde 1989).

If these fights are so costly for both species, why do they happen? How do *C. foveoli* colonies benefit from them? The first explanation could be that they eliminate an eventual food competitor. Nevertheless, different lines of evidence contradict this hypothesis. On the one hand, these attacks do not eliminate *C. ibevica* colonies, nor do they even distance them from *C. foveoli* nests. In fact, the effect of *C. foveoli* on *C. ibevica* populations does not seem to be at all important. Populations of both species are in a certain equilibrium: at the La Paloma site, where a long-term population study is being conducted (X. Cerde and J. Retana, in preparation), the number of *C. ibevica* nests remains more or less constant in spite of the attacks by *C. foveoli*. Moreover, *C. ibevica* cannot be considered a true competitor of *C. foveoli*, because natural differences in diet and activity rhythms between the two species (Retana et al. 1987; Cerde 1988; Cerde and Retana 1988) are maintained when all *C. ibevica* colonies are eliminated from an exclusion area: rates of prey and liquid food collection by *C. foveoli* nests in the exclusion zone were similar to those found in the control zone with *C. ibevica*, and the activity rhythms of *C. foveoli* did not change in the absence of *C. ibevica*. This pattern does not follow other cases where ant species truly compete for food and there is a real increase in food exploitation when the potential competitor is absent (Anderzen and Patel 1994; Perfecto 1994). Although the monitoring of diet and foraging activity alone is probably not sufficient to exclude food competition between the two species (data about the effect of exclusion of *C. ibevica* on the brood production of *C. foveoli* colonies should also be of interest at this point, but they are not available for the present study), the results obtained suggest that the hypothesis of competition for food does not really explain the interference interactions observed in this study.

The hypothesis of competition for a nest site is much better supported. Both in the laboratory and in the field, the most frequent outcome of these aggressive interactions is the occupation of the *C. ibevica* nest by *C. foveoli*. In ants, interspecific nest occupation, after extermination of the original nest population, generally takes place

by direct aggression of the intruder species (Czechowicz 1975; MacKay and MacKay 1982). This behavior may be highly advantageous for *C. foveoli*. As has been shown in the digging experiment, *C. foveoli* is much less skillful at excavating than *C. ibevica*. The species of the genus *Cataglyphis* are adapted to life in sandy areas (e.g., deserts and other arid zones), and they have both morphological (wide mandible opening, long and hairy palps) and behavioral adaptations (coordinated and quick movements of their long legs) to extract soil particles and excavate a new nest. Since the structure of nests of the two species in the field is very similar (personal observations), *C. foveoli* colonies may benefit from these aggressive interactions with *C. ibevica* and, with a limited cost (several dead workers and a few days with lower foraging activity), obtain new nest sites in a much shorter period of time than it would take the workers to excavate them. In areas where *C. ibevica* is absent, *C. foveoli* colonies are similar in size and ecological features to those observed in this study, but they do not attack nests of other species, even though they coexist with other *Cataglyphis* species, such as *Cataglyphis curvator* (Cerde et al. 1997). Differences in soil texture and other related characteristics found between these areas and those of the present study (personal observations) could be one of the reasons explaining the different behavior observed.

An additional interest of this study is the fact that this aggressive interaction involves two subordinate species in the dominance hierarchy (Cerde et al. 1997). In the majority of cases cited in the literature (but see Czechowicz 1985; Heinze and Lipzki 1990), nest invaders are very aggressive, dominant ants in their habitats, which attack and destroy the nests of less aggressive, subordinate species under a variety of conditions (Nilsson 1976; LaMont and Topol 1981; MacKay and MacKay 1982; Droual 1983, 1984). Nevertheless, this study shows that this kind of interference interaction is also found between subordinate, apparently nonaggressive species. This is especially important in the open Mediterranean habitat similar to those where this study has been carried out, where subordinates are far more dominant in the ecosystem than might be expected from their relative abundance and fighting abilities (Cerde et al. 1997; Croz et al. 1997).

Acknowledgements Thanks are due to Dolor Company and Carle Castell for their help in field work. Many other people helped and encouraged us during the work: at the La Paloma site, the family Aroca showed us great hospitality; Abdallah Dahbi generously donated some *C. ibevica* specimens; Alberto Tinaut dissected and prepared ant specimens, and Rocio Requerey provided us with some bibliographic references. This research was partly funded by DGICYT project PB91-0114 to Xim Cerde.

References

- Adam ES (1994) Territory defense by the ant *Azteca trivirgata*: maintenance of an arboreal ant mosaic. *Oecologia* 97: 202–208

- Alzina A, Cerda X, Retana J, Bozch J (1988) Foraging ecology of the aphid-tending ant *Camponotus caryocaryus* (Hymenoptera: Formicidae) in a savanna-like grassland. *Misc Zool* 12: 195–204
- Anderzen AN, Patel AD (1994) Meat ants as dominant members of Australian communities: an experimental test of their influence on the foraging success and forager abundance of other species. *Oecologia* 98: 15–24
- Bank NA, Williams DF (1989) Competitive displacement of *Pavlovichia longicornis* (Latreille) (Hymenoptera: Formicidae) from bait by fire ants in Matto Grosso, Brazil. *J Entomol Sci* 24: 381–391
- Bhatkar A, Whitcomb NH (1970) Artificial diet for rearing various species of ants. *Fla Entomol* 53: 229–232
- Cerda X (1988) Food collection by *Cataglyphis ibeica* (Em.) (Hymenoptera, Formicidae). *Ann Zool* 41: 515–525
- Cerda X (1989) La policalia y el transporte mutuo en la hormiga *Cataglyphis ibeica* (Emery, 1906). PhD thesis, Autonomous University of Barcelona
- Cerda X, Retana J (1988) Influencia de los factores ambientales sobre la actividad diaria de recolección de la hormiga *Cataglyphis ibeica* (Hym.: Formicidae). *Anal Biol* 15: 75–82
- Cerda X, Retana J (1992) A behavioural study of transporter workers in *Cataglyphis ibeica* ant colonies (Hymenoptera Formicidae). *Ethol Ecol Evol* 4: 359–374
- Cerda X, Bozch J, Alzina A, Retana J (1988) Dietary spectrum and activity patterns of *Aphaenogaster zenilis* (Hymenoptera: Formicidae). *Ann Soc Entomol Fr* 24: 69–75
- Cerda X, Retana J, Cruz S (1997) Thermal disruption of transitive hierarchies in Mediterranean ant communities. *J Anim Ecol* 66: 363–374
- Cruz S (1986) Contribució al estudi de l'etologia i l'ecologia de *Pogonomyrmex ruginervis* (Nylander) (Hymenoptera: Formicidae). Tesis de Licenciatura, Autonomous University of Barcelona
- Cruz S, Retana J, Cerda X (1997) Spatial and temporal variations in the activity patterns of Mediterranean ant communities. *Ecoscience* 4: 269–278
- Czechowicz N (1975) Bionomics of *Pogonomyrmex* (Coptoformica) *pseudosulcatus*. *Ann Zool* 33: 273–285
- Czechowicz N (1985) Competition between *Wyvimica laevigata* Nyl. and *Saizius nigiv* (L.) (Hymenoptera, Formicoidea). *Ann Zool* 39: 153–173
- Dejean A, Akoa A, Djieto-Lordon C, Lenoir A (1994) Mosaic ant territories in an African secondary rain forest (Hymenoptera: Formicidae). *Sociobiology* 23: 275–292
- Droual R (1983) The organization of nest evacuation in *Pheidole* *dezeutovi* Wheeler and P. Hyatt Emery (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 12: 203–208
- Droual R (1984) Anti-predator behaviour in the ant *Pheidole* *dezeutovi*: the importance of multiple nests. *Anim Behav* 32: 1054–1058
- Fox BJ, Fox MD, Archer E (1985) Experimental confirmation of competition between two dominant species of *Iridomyrmex* (Hymenoptera: Formicidae). *Aust J Ecol* 10: 105–110
- Gordon DM (1988) Nest-plugging: interference competition in desert ants (*Noromezzus cockerelli* and *Pogonomyrmex* *bivittatus*). *Oecologia* 75: 114–118
- Greenzlade PJM (1971) Interspecific competition and frequency change among ants in Solomon Island coconut plantations. *J Appl Ecol* 8: 323–352
- Greenzlade PJM (1976) The meat ant *Iridomyrmex purpureus* (Hymenoptera: Formicidae) as a dominant member of ant communities. *J Aust Entomol Soc* 15: 237–240
- Haering R, Fox BJ (1987) Short-term coexistence and long-term competitive displacement of two dominant species of *Iridomyrmex*: the successional response of ants to regenerating habitats. *J Anim Ecol* 56: 495–507
- Heinze J, Lipzki N (1990) Fighting and usurpation in colonies of the Palearctic ant *Septothorax gredleri*. *Naturwissenschaften* 77: 493–495
- Holldobler B (1979) Territories of the African weaver ant (*Oecophylla longinoda* (Latreille)). A field study. *Z Tierpsychol* 51: 201–213
- Holldobler B (1982) Interference strategy of *Iridomyrmex* *pseudosulcatus* during foraging. *Oecologia* 52: 208–213
- Holldobler B (1983) Territorial behavior in green tree ant (*Oecophylla* *zavagadina*). *Biotropica* 15: 241–250
- Holldobler B (1984) Communication during foraging and nest-relocation in the African zinc ant, *Paltothyreus* *tavazatus*. *Z Tierpsychol* 65: 40–52
- Holldobler B, Lumden CJ (1980) Territorial strategies in ants. *Science* 210: 732–739
- Holldobler B, Nilsson EO (1990) The ants. Springer, Berlin Heidelberg New York
- Human KG, Gordon DM (1996) Exploitation and interference competition between the invasive Argentine ant, *Sinipithema* *humile*, and native ant species. *Oecologia* 105: 405–412
- Ito Y (1986) Social behaviour of *Ropalidia* *fasciata* (Hymenoptera: Vespidae) females on satellite nests and on a nest with multiple combs. *J Ethol* 4: 73–80
- LaMont B, Topor H (1981) Avoiding predation by army ants: defensive behaviour of three ant species of the genus *Camponotus*. *Anim Behav* 29: 1070–1081
- Mabeliz AA (1984) Interference between wood ants and other ant species (Hymenoptera Formicidae). *Neth J Zool* 34: 1–20
- MacKay N, MacKay N (1982) Coexistence and competitive displacement involving two native ant species. *Southwest Nat* 27: 135–142
- Moglich MHJ, Alpert GD (1979) Stone dropping by *Conomyrma* *bicolor* (Hymenoptera: Formicidae): a new technique of interference competition. *Behav Ecol Sociobiol* 6: 105–113
- Perfecto I (1994) Foraging behavior as a determinant of asymmetric competitive interaction between two ant species in a tropical agroecosystem. *Oecologia* 98: 184–192
- Retana J, Cerda X (1995) Agonistic relationships among sympatric Mediterranean ant species. *J Insect Behav* 8: 365–380
- Retana J, Bozch J, Alzina A, Cerda X (1987) Foraging ecology of the nectarivorous ant *Camponotus* *foveoli* (Hymenoptera, Formicidae) in a savanna-like grassland. *Misc Zool* 11: 187–193
- Retana J, Cerda X, Alzina A, Bozch J (1988) Field observations of the ant *Camponotus* *zygoticus* (Hym.: Formicidae): diet and activity patterns. *Acta Oecol Oecol Gen* 9: 101–109
- Riechert SE (1988) The energetic costs of fighting. *Am Zool* 28: 877–884
- Room PM (1971) The relative distribution of ant species in Ghana's cocoa farms. *J Anim Ecol* 40: 735–751
- Samways MJ (1982) Soil dumping by *Wyvimica* *natalensis* (Smith) (Hymenoptera: Formicidae) as a competitive advantage over other ant species. *Phytophactica* 14: 3–5
- Samways MJ (1983) Community structure of ants (Hymenoptera Formicidae) in a series of habitats associated with citrus. *J Appl Ecol* 20: 833–847
- Savolainen R (1990) Colony success of the subterranean ant *Pogonomyrmex* *polyctenus*. *Ecol Entomol* 15: 1–10
- Schoener TN (1968) The Anolis lizard of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704–726
- Smallwood J (1982) Nest relocation in ants. *Insect Soc* 29: 138–147
- Strazmann JE (1981) Evolutionary implications of early male and satellite nest production in polytrophic exclamation colony cycles. *Behav Ecol Sociobiol* 8: 55–64
- Vepäläinen K, Savolainen R (1990) The effect of interference by formicine ants on the foraging of *Wyvimica*. *J Anim Ecol* 59: 643–654
- Nilsson EO (1976) The organization of colony defense in the ant *Pheidole* *dentata* Mayr (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 1: 63–81
- Nilsson EO (1990) Success and dominance in ecosystems: the case of the social insects. *Ecology Institute, Oldendorf/Luhe*
- Yamaguchi T (1992) Interspecific interference for nest sites between *Septothorax* *congruus* and *Wonomomyrmex* *intusus*. *Insect Soc* 39: 117–127