Journal of Chemical Ecology, Vol. 22, No. 12, 1996

SOCIAL CLOSURE, AGGRESSIVE BEHAVIOR, AND CUTICULAR HYDROCARBON PROFILES IN THE POLYDOMOUS ANT *Cataglyphis iberica* (HYMENOPTERA, FORMICIDAE)

ABDALLAH DAHBI,[1,*] XIM CERDÁ,[1,2,5] ABRAHAM HEFETZ,[1,3] and ALAIN LENOIR[1,4]

[1] *Laboratoire d'Ethologie Expérimentale et Comparée, URA 2214*
Université Paris Nord
93430 Villetaneuse, France

[2] *Unitat d'Ecologia, Facultat de Ciències*
Universitat Autónoma de Barcelona
08193 Bellaterra, Barcelona, Spain

[3] *Department of Zoology, George S. Wise Faculty of Life Science*
Tel Aviv University
Ramat Aviv, Tel Aviv 69978, Israel

[4] *Laboratoire d'Ethologie et Pharmacologie du Comportement*
Faculté des Sciences et Techniques, 37200 Tours, France

[5] *Present address: Estacion Biologica de Donãna (CSIC), Apdo.1056, E-41080 Sevilla, Spain*

(Received September 7, 1995; accepted July 9, 1996)

Abstract—Nestmate recognition was studied in the polydomous ant *Cataglyphis iberica* (Formicinae) in the laboratory. The study examined six colonies collected from two different populations 600 km apart in the Iberian peninsula (Barcelona and Murcia). Introduction of an alien worker into an allocolonial arena always ended in death to the intruder, demonstrating that in this species societies are extremely closed. Dyadic encounters composed of individuals from different colonies in a neutral arena confirmed the existence of high aggression between allocolonial individuals. We also investigated variability in the composition of the major cuticular hydrocarbons between the colonies used in the behaviorial tests. There were marked quantitative differences between the profiles of ants from the two populations, suggesting that the populations are completely segregated. Cuticular profiles within a population tended to be more similar, but were nevertheless colony specific. The degree of colony closure in *C. iberica* seemed to be independent

---

*To whom correspondence should be addressed.

of geographic distance since aggression between the colonies was always at its maximum, irrespective of their population origin.

Key Words—Ants, Formicinae, polydomy, nestmate recognition, aggression, cuticular hydrocarbons, colony closure, *Cataglyphis iberica*.

INTRODUCTION

Social organization in ants is based on, among other things, colony closure that preserves its social integrity and prevents intrusion by individuals alien to the society. This necessitates a capacity to recognize and discriminate between familiar and unfamiliar individuals. Such discrimination generally induces aggression towards the unfamiliar intruder. As early as 1904, Fielde (1904) hypothesized a chemical role in recognition. Howse (1975) suggested that this discrimination ability was based essentially on a chemical signature that each member of the colony carries on its cuticle, a hypothesis that was subsequently confirmed by experimental work (reviewed by Howard, 1993; Lorenzi et al., 1996). Experiments in which alien cuticular extracts applied to workers elicited aggression towards them by their nestmates lent credence to the role of cuticular lipids in colony recognition (Bonavita-Cougourdan et al., 1987; Nowbahari et al., 1990; Henderson et al., 1990). Nestmate recognition cues can be determined genetically (Vander Meer et al., 1985; Ross et al., 1987; Provost, 1991), but may also include environmental substances that blend into the colony odor (Jutsum et al., 1979; Obin, 1986; Obin and Vander Meer, 1988). Congruency was found between the hydrocarbon composition of postpharyngeal gland contents and those of the cuticular washes (Bagnères and Morgan, 1991; Do Nascimento et al., 1993). Recent studies pointed to the role of the postpharyngeal gland in storing and mixing the recognition chemicals and reapplying them on the cuticle, creating a unified colony odor (Soroker et al., 1994, 1995).

Earlier studies with *Cataglyphis cursor* have shown a correlation between intercolonial aggression and the geographic distance between colonies (Nowbahari and Lenoir, 1984; Nowbahari et al., 1990). In this species, whose colonies multiply by fission, allocolonial workers that originate from neighboring nests are readily accepted, whereas workers originating from distant colonies are always rejected.

Cataglyphis iberica is a monogynous and polydomous species that is limited to the Iberian peninsula (Tinaut and Plaza, 1989; Cerdá and Retana, 1992). Each colony is composed of several satellite nests, between which there is an exchange of individuals through adult transport. Its biology is typical of the majority of species in this genus: it is a diurnal scavenger ant species that is active during the hottest period of the day (Cerdá, 1988; Cerdá and Retana, 1988).

In this study, we tested colonial closure in *C. iberica* and compared intercolonial aggression in relation to divergence in their cuticular hydrocarbon profiles and the geographic distances separating the colonies.

METHODS AND MATERIALS

Origin and Rearing of Colonies. This study was conducted with six colonies collected from two different populations in Spain, about 600 km apart. Three colonies were collected near Barcelona (population B): colony B1, collected from Bellaterra, was comprised of three satellite nests containing a total of 1650 workers. Colonies B2 and B3 were both collected from Sant Cugat (3 km away from Bellaterra), each of which was comprised of two satellite nests containing a total of 1918 and 975 workers, respectively. Three additional colonies were collected in the province of Murcia (population M). Colony M1 was from La Paloma (near Murcia) and included two satellite nests with a total of 1260 workers. Colonies M2 and M3 were collected from Cabo de Gata (about 200 km South from La Paloma) each composed of a single nest containing 450 and 325 workers, respectively.

In the laboratory, the colonies were reared in plastic boxes (11.5 × 8.0 × 2.5 cm) in which the interior relative humidity was maintained at 50%. Each satellite nest occupied one box, but all satellites belonging to the same colony were connected by plastic tubes to a common foraging arena (35 × 35 cm). As the species is very thermophilic (Cerdá and Retana, 1988), the arena was heated to 25 ± 2°C by a lamp to allow adequate temperatures for foraging activity. Food (meal worms, cricket larvae, honey-apple mixture) was provided three times a week and water *ad libitum*. The nests were maintained at 10:14 D:L photoperiod.

Introduction of Workers into an Allocolonial Arena. For each test one worker was introduced into an allocolonial foraging arena that was lined with filter paper. Tests were performed with at least a 1-hr break between replicates, and the filter paper was changed for each replicate. The behavioral interactions with the resident ants were observed while measuring two time variables: the latency before the first attack (first attack time), and the time it took to kill the introduced worker (death time). The number of resident workers that were present in the arena was monitored at the beginning of each test. All tests were conducted between 10:00 and 16:00 hr during the daily activity period of the ants when foragers were present in the arena. Each test lasted until the introduced worker was killed. The tests conducted included all possible combination of the six colonies: B × B (43 tests), M × M (52 tests), and B × M (22 tests).

Dyadic Encounters. Tests of internidal aggression consisted of encounters between two alien ants in a neutral arena made up of a circular plastic box (8 cm in diameter) coated on the inner walls with Fluon. Before each test the arena was thoroughly cleaned with alcohol. Each encounter lasted for 10 min and involved individuals originating from different colonies that were either taken from the same population (type I encounters, six combinations) or taken from different populations (type II encounters, nine combinations) (see Table I below). Initially, five replicates were performed for each combination, which involved different individuals in order to avoid familiarization or cross-contamination by cuticular lipids. The behavior of only one of the contestants (alternatively selected) was recorded in each test, and aggression was calculated as relative frequencies of aggressive acts out of the total interactions observed during the encounter. The following behaviors were considered as aggression: opening of the mandibles, biting, or flexing the gaster. On the other hand, mutual investigation and submissive posture were considered to be neutral or amicable acts. In a few of the tests (~ 12%) there were neither contacts nor interactions between the ants, and the ants displayed mutual avoidance. Such indifference is also often observed in the field. These cases were excluded from further calculations to avoid an artificial lowering of the magnitude of aggression and therefore bias the statistics.

Chemical Analysis. For the chemical analyses, postpharyngeal glands of 30 ants from each population were dissected under distilled water and immediately immersed in 100 μl of pentane for extraction. The pooled samples were analyzed by coupled gas chromatography–mass spectrometry (Finnigan quadrupole or Fisons MD800 quadrupole) in the EI and CI (using methane as reagent gas) modes. The samples were run on an HP-5 fused silica capillary column that was heated from 150°C to 250°C at a rate of 5°C/min, or alternatively on a DB-5 fused silica capillary column that was temperature programmed from 120°C to 300°C at 3°C/min with an initial hold of 3 min. The various hydrocarbons were identified by their fragmentation patterns as compared to published spectra (Nowbahari et al., 1990; Bagnères et al., 1991).

The contents of the postpharyngeal and cuticular washes were compared by gas chromatography using the elution pattern and including reference compounds.

To compare cuticular hydrocarbon profiles between colonies used in the behavioral studies, cuticular washes from individuals were analyzed by gas chromatography. Six individuals were taken at random from each of the colonies and individually analyzed: each ant was washed for 10 min in 1 ml of acetone. The solution was then dried by nitrogen and the residue was redissolved in 30 μl acetone, of which 2 μl were injected into a gas chromatograph (Delsi 300) equipped with a capillary column (Chrompak CPSIL 5 WCOT 25 m × 0.22 mm in diameter), temperature programmed from 100°C to 280°C at a rate of 3°C/min). Peak integration was accomplished with an ENICA 21 integrator.

Calculations and Statistical Methods. All calculations and comparisons were made by using the mean ± SE. The α value for all the statistical tests used (discriminant analysis, Fisher's PLSD, χ^2, Mann-Whitney, and Pearson's) was less than 5%. The comparison of cuticular profiles of individuals from the studied colonies was performed by a discriminant analysis (Statistica for Windows) based on the compounds with a relative intensity above 1% in at least one of the samples (a total of 33 compounds).

RESULTS

Aggression Towards Ants Introduced into Allocolonial Arena. All ants introduced into an allocolonial arena were eliminated without a single case of adoption. The resident ants in the arena were very aggressive towards the alien intruders and engaged in mortal attack as soon as the intruder ant was detected in the arena. The average latency to the first attack was 19.1 ± 3.3 sec, and the average time that elapsed until the alien ant was killed was 17.0 ± 2.3 min. Significant relationships were found between the two variables (the first attack time and the death time) and the number of foragers present in the arena (Pearson's $r = 0.25$, $P = 0.007$ in both cases), but the low r^2 ($=0.06$) value indicated that the level of aggressive response was only weakly dependent on the number of resident foragers in the arena.

In addition, the geographic distance between the colonies did not influence the latency of the first attack (Pearson's $r = 0.11$, NS), but geographic distance was weakly but significantly correlated with death time ($r = 0.37$, $P < 0.001$). The greater the geographic distance between the tested colonies, the quicker the alien ants were eliminated.

Aggression during Dyadic Encounters. In eight of the 75 dyadic encounters conducted there were no interactions between ants. These ants neither moved nor was there was any contact between them. These encounters were therefore excluded from further calculations in order to avoid any artificial reduction in the mean aggressive response. In the 67 encounters taken for analysis, workers of *C. iberica* always engaged in aggressive interactions after a short antennal contact, and rarely manifested neutral or amicable behavior. This is reflected in the high value of the frequency of aggressive acts calculated for all the encounters (0.70 ± 0.03).

The frequency of aggressive acts was rather homogeneous between the various combinations, ranging from 0.48 for the encounters involving ants from colonies B3 and M1 to 0.87 for the encounters between ants from colonies B2 and B3. When tests are grouped as type I encounters (workers originating from different colonies from the same population) and type II encounters (workers originating from colonies from different populations), no differences were found between the mean values of aggressive frequencies for each type of dyadic encounter (Table 1, U Mann-Whitney test, $P > 0.1$).

TABLE 1. AGGRESSIVE FREQUENCIES (MEAN ± SE) FOR TYPE I AND II ENCOUNTERS[a]

Dyadic tests	Aggression frequency
Type I tests	
B1-B2(5)	0.69 ± 0.11
B1-B3(5)	0.63 ± 0.14
B2-B3(5)	0.87 ± 0.08
B-B(15)	0.73 ± 0.07[a]
M1-M2(4)	0.71 ± 0.12
M1-M3(3)	0.54 ± 0.12
M2-M3(5)	0.72 ± 0.14
M-M(12)	0.67 ± 0.07[a]
Type II tests	
B1-M1(5)	0.58 ± 0.17
B1-M2(5)	0.73 ± 0.08
B1-M3(4)	0.85 ± 0.10
B2-M1(5)	0.73 ± 0.08
B2-M2(5)	0.70 ± 0.12
B2-M3(4)	0.86 ± 0.07
B3-M1(4)	0.48 ± 0.15
B3-M2(4)	0.76 ± 0.09
B3-M3(4)	0.65 ± 0.08
B-M(40)	0.70 ± 0.04[a]

[a] No differences were found between intrapopulation mean values (Fisher's PLSD, $P > 0.1$).

We further tested whether the levels of intercolonial aggression within a population differed from that between populations. The frequency of aggressive acts in the tests within a population (0.73 ± 0.07 and 0.67 ± 0.07 for populations B and M, respectively) was as high as the frequencies in the tests between populations (0.70 ± 0.04) (Table 1, Fisher's PLSD, $P > 0.10$).

An examination of the workers after an hour of a dyadic encounter showed that despite the high aggression between the ants, the dyadic interactions rarely ended in death (18 deaths of 134 tested workers) or injury (24 injured of 134) to one or both ants. The number of injured and killed workers was not different between type I and type II encounters ($\chi^2 = 0.064$, $P = 0.8$).

Chemical Analysis. The postpharyngeal gland exudates of ants from the two populations contained almost exclusively saturated hydrocarbons, including *n*-alkanes and mono- and dimethyl alkanes ranging from C_{12} to C_{34}. There was an additional series of monomethyl and dimethyl *n*-alkanes of higher molecular weight, but the intensities of the peaks did not allow proper identification (Table 2). The hydrocarbon profiles from ants belonging to populations B and M were qualitatively similar but differed quantitatively. The dominant compounds in the

TABLE 2. COMPOUNDS IDENTIFIED FROM POSTPHARYNGEAL GLANDS DISSECTED FROM INDIVIDUALS BELONGING TO NESTS COLLECTED FROM BARCELONA OR MURCIA POPULATIONS[a]

Compounds[b]	Relative amount		Compounds	Relative amount	
	Barcelona	Murcia		Barcelona	Murcia
Dodecane	t	t	4 m C_{24}	t	t
Tridecane	t	t	C_{25}	t	t
11 m C_{13}	t	t	11 m C_{25}	t	t
Pentadecane	t	t	7 m C_{25}	t	t
Hexadecane	t	t	5 m C_{25}	t	t
6 m C_{16}?	t	t	11,15 dm C_{25}	t	t
4 m C_{16}	t	t	3 m C_{25}	t	t
C_{17}	t	t	5,9 dm C_{25}	t	t
8,12 dm C_{16}	t	t	*x*,12 dm C_{25}	t	t
5 m C_{17}	t	t	C_{26}	t	t
4 m C_{17}	t	t	11 + 13 + 15 m C_{26}	t	t
3 m C_{17}	t	t	6 m C_{26}	t	t
C_{18}	t	t	5 m C_{26}	t	t
8,12 dm C_{18}	t	t	4 m C_{26}	t	t
C_{19}	t	t	5,9 + 5,13 cm C_{26}	t	t
C_{20}	t	t	5,11 dm C_{26}	t	t
Oleic acid	t	t	4,6 dm C_{26}	t	t
C_{22}	t	t	4,10 + 4,12 dm C_{26}	t	t
11 m C_{23}	t	t	C_{27}	t	2.88 ± 2.72
10 m C_{23}	t	t	11 + 13 m C_{27}	t	5.19 ± 1.37
5 m C_{23}	t	t	7 m C_{27}	t	t
3 m C_{23}	t	t	5 m C_{27}	t	t
C_{24}	t	t	11,15 dm C_{27}	t	t
6 m C_{24}	t	t	16,18 dm C_{27}	t	t
5 m C_{24}	t	t	7,11 dm C_{27}	t	t

TABLE 2. CONTINUED

Compounds[b]	Relative amount		Compounds	Relative amount	
	Barcelona	Murcia		Barcelona	Murcia
3 m C_{27}	t	4.34 ± 0.62	x,y dm C_{29}	t	t
5,9 dm C_{27}	t	t	3,9 dm C_{29}	4.08 ± 1.04	2.32 ± 0.54
5,13 dm C_{27}	t	t	C_{30}	t	t
C_{28}?	2.02 ± 1.71	1.04 ± 1.01	6 m C_{30}	2.41 ± 1.15	1.92 ± 1.31
12 m C_{28}	t	6.21 ± 2.40	5 m C_{30}	t	t
11 + 13 + 15 m C_{28}	t	2.88 ± 0.31	4 m C_{30}	2.59 ± 0.64	1.39 ± 0.35
3,7 dm C_{27}	t	t	9,15 dm C_{30}	t	t
mix of monomethyl C_{28}	t	t	x, 8 dm C_{30}	t	t
			4,8 dm C_{30}	t	t
6 m C_{28}	t	t	6,14 + 4,14 dm C_{30}	t	t
5 m C_{28}	t	t	4,10 dm C_{30}	t	t
4 m C_{28}	t	1.19 ± 0.49	5,9 + 5,11 + 5,14 dm C_{30}	t	t
3 m C_{28}	t	t	C_{31}	4.76 ± 2.68	t
5,11 dm C_{28}	t	t	15 m C_{31}	3.06 ± 1.04	3.71 ± 0.62
4,8 dm C_{28}	t	t	9 m C_{31}	2.86 ± 0.38	t
C_{29}	5.87 ± 3.73	7.51 ± 6.46	7 m C_{31}	2.79 ± 0.83	t
3,7 + 3,9 dm C_{28}	t	t	5 m C_{31}	2.66 ± 1.04	t
11 + 13 + 15 m C_{29}	3.42 ± 1.08	15.19 ± 2.24	11,15 dm C_{31}	8.29 ± 2.35	2.64 ± 0.82
9 m C_{29}	1.07 ± 0.40	3.38 ± 0.50	11,17 + 12,16 dm C_{31}	1.37 ± 0.39	t
7 m C_{29}	1.31 ± 0.31	1.06 ± 0.89	7,15 dm C_{31}	1.07 ± 0.79	t
5 m C_{29}	4.42 ± 1.59	3.73 ± 0.78	3 + 4 + 5 m C_{32}	t	t
11,13 dm C_{29}	1.27 ± 0.55	7.24 ± 0.88	7,11 dm C_{32}?	1.82 ± 0.39	t
7,17 dm C_{29}	1.37 ± 0.73	t	C_{33}?	t	t
7,11 dm C_{29}	t	t	12, x dm C_{32}	1.18 ± 0.54	t
3 m C_{29}	9.82 ± 3.71	5.95 ± 1.67	4,22 dm C_{32}	3.00 ± 0.83	t
5,9 dm C_{29}	1.42 ± 0.45	1.84 ± 0.33	x,15 dm C_{32}	1.96 ± 1.24	t

mix of dm C_{32}	1.67 ± 0.60	t	12 m C_{33}	t	t
x,16 dm C_{32}	t	t	13,17 dm C_{33}	2.13 ± 0.51	t
6,30 dm C_{32}	t	t			

---

[a] Compounds with a relative amount that was less than 1% were marked as traces (t). The identity of compounds followed by a question mark is uncertain. The mean values (±SD, $N = 9$) given in the table are calculated from the cuticular hydrocarbon profiles of individuals used in the discriminant analysis.

[b] m = methyl; dm = dimethyl.

ants from both populations were nonacosane and a series of monomethyl and dimethyl nonacosanes. Ants from the Murcia population were distinguishable from those from the Barcelona population by having a larger proportion of heptacosane and octacosane compounds, notably C_{27} and its 13-, 11-, and 3-methyl branched derivatives, 12-methyl C_{28} and a mixture of 11- + 13- + 15-methyl C_{28}. These were present only in traces in individuals from population B. Finally, Barcelona ants were distinguishable by having a larger proportion of hydrocarbons with heavier molecular weight corresponding to hentriacontane, a series of monomethyl and dimethyl hentriacontane, and dimethyl dotriacontane.

Cuticular hydrocarbon profiles of the 36 ants from the six colonies were analyzed by discriminant analysis (Figure 1). A plot of the first and the second variables shows that individuals belonging to the same population clustered together forming two clearly separated groups. These two groups were separated mostly by the first discriminant variable. Within each population, individual grouping according to colony origin is apparent, and colonies were well separated by the second discriminant variable. The compounds that had an important weight in the analysis were heptacosane and a mixture of its 11-, 13-methyl-branched derivatives and 12-methyl C_{28}. It is worth noting that colony M1, which clustered distantly from M2 and M3 based on the hydrocarbon profile,

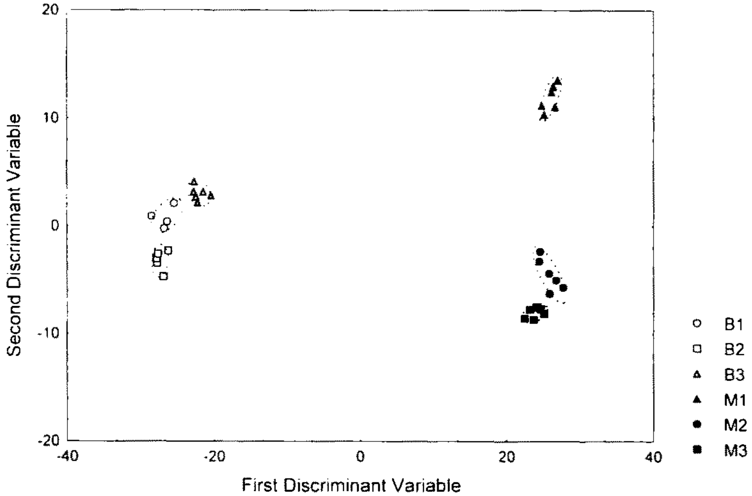

FIG. 1. A plot of the first two principal variables in the discriminant analysis of cuticular hydrocarbons of the six colonies of *Cataglyphis iberica*. Each colony group is surrounded by the confidence ellipse ($P < 0.05$).

was also geographically separated by 200 km from these two colonies (which were collected from the same locality).

We also conducted a discriminant analysis within each population on the basis of the same peaks. The results confirmed those shown in Figure 1. For the 18 ants analyzed on the basis of their cuticular profile within each population, individuals clearly clustered together according to their colony origin. Within population B, the compounds that had an important discriminant impact were a mixture of 15-, 13-, 11-, and 5-methyl C_{29} and 5,9-dimethyl C_{29}; while for population M, the discriminant compounds were 3-methyl C_{27}, 4-methyl C_{28} and 7-methyl C_{29}. This indicates that profile disparities between populations (B–M) and within populations (B–B or M–M) are not due to the same compounds.

DISCUSSION

Polydomous ant species are generally polygynous, with a low nestmate recognition system that seems to be the consequence of the low intracolonial relatedness (Hölldobler and Wilson, 1977; Breed and Bennett, 1987; Bourke and Franks, 1995). This low nestmate recognition system was observed, for example, in *Linepithema humile* (*Iridomyrmex humilis*) (Markin, 1968; Benois, 1973; Keller and Passera, 1989), *Amblyopone pallipes* (Traniello, 1982), and *Myrmica incompleta* (Lenoir et al., 1989). In *C. iberica*, societies are polydomous, but with a single queen per colony. Our results show that these colonies are very closed towards alien conspecifics. Because the colonies are monogynous, we suggest that this intolerance may be due to a high intracolonial genetic relatedness. However, monogyny is not systematically associated with a high colonial closure. In *C. cursor*, which is monogynous but monodomous (Cagniant, 1976), very little aggressive behavior is observed when the individuals come from the same site (Nowbahari and Lenoir, 1984). This low level of aggressive behavior can be explained by its mode of colony foundation, which is achieved through fission, resulting in high genetic relatedness between proximate colonies (Lenoir et al., 1988). The high level of colonial closure in *C. iberica* might have originated from the mode of colony foundation. Some field observations suggest that in this species there is an independent mode of colony foundation (X. Cerdá, unpublished data), which, contrary to fission, results in genetic and geographic proximity being opposed. Thus, even neighboring colonies of *C. iberica* may be genetically dissimilar.

The comparative analysis of cuticular washes revealed quantitative differences in hydrocarbons between the tested colonies. Colonies from the same population (B or M), although distinct from each other, had more similar patterns than between populations. This suggests that nests from Barcelona and Murcia comprise disparate populations. There is also an indication that the disparity between nests within a population may increase with geographic distance. This was evident from the higher distance in the discriminant analysis (based on the hydrocarbon profile) of one nest from Murcia that was located 200 km away from the others. Moreover, there is no geographical barrier between Barcelona and Murcia, and cuticular profiles of ants collected between the two populations show a quantitative gradual divergence of profiles (Dahbi, unpublished data).

We may link the disparities in cuticular hydrocarbons with aggression exhibited by these ants towards alien ants. We base our assumption on the "Gestalt" model. The individuals that were used in recognition tests are nestmates of those analyzed through chromatography, and we assume the presence of a common colonial odor for workers of the same colony (Soroker et al., 1994). The fact that aggression between colonies was at a maximum irrespective of the degree of similarity in hydrocarbons profile suggests that even the small differences exhibited between the colonies of the Barcelona population are above the recognition threshold and suffice to elicit a full response. This hypothesis, however, has to be tested by using pure hydrocarbons at various quantitative combinations.

Acknowledgments—We thank Andrea Dejean for the first English translation and Nomi Paz for final proof reading. This work was supported by a grant from MEC/MRT (FR91) to Xim Cerdá, and by two French-Spanish cooperation projects (Picasso, Acciones Integradas HF93-133B and HF94-345B).

REFERENCES

BAGNÈRES, A.-G., and MORGAN, E. D. 1991. The postpharyngeal glands and the cuticle of Formicidae contain the same characteristic hydrocarbons. *Experientia* 47:106–111.

BAGNÈRES, A.-G., ERRARD, C., MULHEIM, C., JOULIE, C., and LANGE, C. 1991. Induced mimicry of colony odors in ants. *J. Chem. Ecol.* 17:1641–1664.

BENOIS, A. 1973. Incidences des facteurs écologiques sur le cycle annuel et l'activité saisonnière de la fourmi d'Argentine *Iridomyrmex humilis* (Mayr) (Hymenoptera, Formicidae), dans la région d'Antibes. *Insectes Soc.* 20:267-296.

BONAVITA-COUGOURDAN, A., CLÉMENT, J.-L., and LANGE, C. 1987. Nestmate recognition: The role of cuticular hydrocarbons in the ant *Camponotus vagus* Scop. *J. Entomol. Sci.* 22:1–10.

BOURKE, A. F. G., and FRANKS, N. 1995. Social evolution in Ants. Princeton University Press, Princeton, New Jersey.

BREED, M. D., and BENNETT, B. 1987. Kin recognition in highly eusocial insects, pp. 243–286, *in* D. J. C. Flecher and C. D. Michener (eds.). Kin Recognition in Animals. John Wiley & Sons, New York.

CAGNIANT, H. 1976. Cycle biologique de la fourmi *Cataglyphis cursor* Fonscolombe. Hymènoptères, Formicidae. *Vie Milieu* 26:277-281.

CERDÁ, X. 1988. Food collection by *Cataglyphis iberica* (Em.) (Hymenoptera, Formicidae). *Ann. Zool.* 41:515-524.

CERDÁ, X., and RETANA, J. 1988. Influencia de los factores ambientales sobre la actividad diaria de recoleccion de la hormiga *Cataglyphis iberica* (EM.) (Hym: Formicidae). *An. Biol.* 15:75-82.

CERDÁ, X., and RETANA, J. 1992. A behavioural study of transporter workers in *Cataglyphis iberica* ant colonies (Hymenoptera, Formicidae). *Ethol. Ecol. Evol.* 4:359-374.

DO NASCIMENTO, N. R. R., BILLEN, J., and MORGAN, E. D. 1993. The exocrine secretions of the jumping ant *Harpegnathos saltator*. *Comp. Biochem. Physiol.* 104B:505-508.

FIELDE, A. M. 1904. Power of recognition among ants. *Biol. Bull. Mar. Biol. Lab.* 7:227-250.

HENDERSON, G., ANDERSEN, J. F., and PHILLIPS, J. K. 1990. Internest aggression and identification of possible nestmate discrimination pheromones in polygynous ant *Formica montana*. *J. Chem. Ecol.* 16:2217-2228.

HÖLLDOBLER, B., and WILSON, E. O. 1977. The number of queens: An important trait in ant evolution. *Naturwissenschaften* 64:8-15.

HOWARD, R. W. 1993. Cuticular hydrocarbons and chemical communication, pp. 179-226, *in* D. W. Stanley-Samuelson and D. R. Nelson (eds.). Insect Lipids: Chemistry, Biochemistry and Biology, University of Nebraska Press, Lincoln.

HOWSE, P. E. 1975. Chemical defenses of ants, termites and other insects: some outstanding questions, pp. 23-40, *in* C. Noirot, P. E. Howse and G. Le Masne (eds.). Pheromones and Defensive Secretions in Social Insects. IUSSI, Dijon, France.

JUTSUM, A. R., SAUNDERS, T. S., and CHERRETT, J. M. 1979. Intraspecific aggression in the leaf-cutting ant *Acromyrmex octospinosus*. *Anim. Behav.* 27:839-844.

KELLER, L., and PASSERA, L. 1989. Influence of the number of queens on nestmate recognition and attractiveness of queens to workers in the Argentine ant *Iridomyrmex humilis* (Mayr). *Anim. Behav.* 37:733-740.

LENOIR, A., QUERARD, L., PONDICQ, N., and BERTON, F. 1988. Reproduction and dispersal in the ant *Cataglyphis cursor* (Hymenoptera, Formicidae). *Psyche* 95:21-44.

LENOIR, A., FRANCOEUR, A., ERRARD, C., and JAISSON, P. 1989. Résultats préliminaires sur le comportement de *Formicoxenus provancheri* en relation avec son hôte *Myrmica incompleta* (Hymenoptera, Formicidae). *Actes Colloq. Insectes Soc.* 5:225-232.

LORENZI, M. C., BAGNÈRES, A.-G., and CLÉMENT, J.-L. 1996. The role of cuticular hydrocarbons in social insects: is it the same in paper-wasps? pp. 178-189, *in* S. Turilazzi and M. J. West-Eberhard (eds.). Natural History and Evolution of Paper-wasps. Oxford University Press, Oxford.

MARKIN, G. P. 1968. Nest relationship of the Argentine ant *Iridomyrmex humilis* (Hymenoptera: Formicidae). *J. Kans. Entomol. Soc.* 41:511-516.

NOWBAHARI, M., and LENOIR, A. 1984. La fermeture des sociétés de la fourmi *Cataglyphis cursor*; relations avec la distance géographique, pp. 457-461, *in* A. De Haro and X. Espadaler (eds.). Processus d'acquisition précoce. Les communications. Serv. Publ. Univ. Auton. Barcelona, SFECA, Bellaterra.

NOWBAHARI, E., LENOIR A., CLÉMENT, J.-L., LANGE, C., BAGNÈRES, A.-G., and JOULIE, C. 1990. Individual, geographical and experimental variation of cuticular hydrocarbons of the ant *Cataglyphis cursor* (Hymenoptera: Formicidae): their use in nest and subspecies recognition. *Biochem. Syst. Ecol.* 18:63-73.

OBIN, M. S. 1986. Nestmate recognition cues in laboratory and field colonies of *Solenopsis invicta* Buren (Hymenoptera: Formicidae): Effect of environment and the role of cuticular hydrocarbons. *J. Chem. Ecol.* 12:1965-1975.

OBIN, M. S., and VANDER MEER, R. K. 1988. Sources of nestmate recognition cues in the imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae). *Anim. Behav.* 36:1361-1370.

PROVOST, E. 1991. Nonnestmate kin recognition in the ant *Leptothorax lichtensteini*: Evidence that genetic factors regulate colony recognition. *Behav. Genet.* 21:151-167.

ROSS, K. G., VANDER MEER, R. K., FLETCHER, D. J. C., and VARGO, E. L. 1987. Biochemical phenotypic and genetic studies of two introduced fire ants and their hybrid (Hymenoptera: Formicidae). *Evolution* 41:280–293.

SOROKER, V., VIENNE, C., and NOWBAHARI, E., and HEFETZ, A. 1994. The postpharyngeal gland as a "gestalt" organ for nestmate recognition in the ant *Cataglyphis niger*. *Naturwissenschaften* 81:510–513.

SOROKER, V., VIENNE, C., and HEFETZ, A. 1995. Hydrocarbon dynamics within and between nestmates in *Cataglyphis niger* (Hymenoptera: Formicidae). *J. Chem. Ecol.* 21:365–378.

TINAUT, A., and PLAZA, J. L. 1989. Situacion taxonomica del género *Cataglyphis* Förster, 1850 en la Peninsula Ibérica. I. Las especies del subgénero *Cataglyphis* Förster (Hym. Formicidae). *Eos* 65:189–199.

TRANIELLO, J. F. A. 1982. Population structure and social organization in the primitive ant *Amblyopone pallipes* (Hymenoptera: Formicidae). *Psyche* 89:65–80.

VANDER MEER, R. K., LOFGREN, C. S., and ALVAREZ, F. M. 1985. Biochemical evidence for hybridization in fire ants. *Fla. Entomol.* 68:501–506.