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Nest separation and the dynamics of the *Gestalt* odor in the polydomous ant *Cataglyphis iberica* (Hymenoptera, Formicidae)

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Abstract In the polydomous ant species *Cataglyphis iberica*, nests belonging to the same colony are completely separated during hibernation. In order to examine whether this separation induces changes both in the hydrocarbon profile and in recognition ability between adult nestmates, we separated groups of workers for several months under two different conditions: at hibernation temperature and at room temperature. At room temperature, recognition remained unchanged but separation led to longer mutual antennations relative to non-separated controls. When half of a colony was placed under hibernation conditions, antennal interactions also increased in duration and a few aggressive interactions emerged between separated ants. This aggressiveness never reached the intercolonial level observed in this species. In both cases, the hydrocarbon profiles showed differences between individuals after separation while remaining homogeneous within each nest. This chemical modification may induce the longer antennations observed. After separated groups were reunited, individuals recovered their previous antennation pattern and a convergence in hydrocarbon profiles was again observed. These concurrent observations suggest that hydrocarbons are transferred between nestmates. In *C. iberica*, the formation of the colonial odor seems to follow the "*Gestalt*" model which allows all satellite nests of a colony to have a common colonial odor. In the field, temporary nest isolation during hibernation may induce divergence between satellites. The role of adult transport in connecting nests during the active season to obtain an efficient *Gestalt* odor is discussed.

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Introduction

Nestmate recognition is important in social insects since it is responsible for the maintenance of the colony integrity against parasites and foreign competitors (Wilson 1971). The chemical nature of recognition cues was alluded to as early as 1904 (Fielde 1904). More recently, many studies have revealed the involvement of cuticular chemical cues, with hydrocarbons representing the major class of chemicals found on the cuticle (see reviews by Hölldobler and Michener 1980; Jaisson 1985; Breed and Bennett 1987; Lenoir et al. in press). Moreover, lures saturated with cuticular extracts proved the role of cuticular lipids in nestmate discrimination and suggested the involvement of cuticular hydrocarbons in this recognition process (Bonavita-Cougourdan et al. 1987; Morel et al. 1988; Henderson et al. 1990; Nowbahari et al. 1990). All these experiments were carried out on ants of the subfamily Formicinae. However, other Hymenoptera species may use different recognition systems involving, for example, polar cuticular lipids (Franks et al. 1990), nesting materials (Breed et al. 1995), or food quality (Jutsum et al. 1979; Obin and Vander Meer 1988).

Discrimination of non-nestmates is possible only if all nestmates carry a specific chemical signal recognized by each. This signal generates a template (Breed and Bennett 1987) which constitutes the memorized reference odor. Each individual can be accepted or rejected from the colony according to the similarity of its odor to the colonial template. Crozier and Dix (1979) presented two models to explain the genetic modalities for the discrimination system (see Crozier and Pamilo 1996). In the "individualistic" model, each member of the colony keeps its own chemical characteristics without transfer of cues between nestmates. This recognition process is

reported mainly in primitive societies containing only a few individuals such as the primitively social bee *Lasioglossum zephyrum* (Greenberg 1979; Buckle and Greenberg 1981), but has also been suggested in socially advanced insects (e.g., *Pseudomyrmex ferruginae*, Mintzer 1982; Mintzer and Vinson 1985). In the *Gestalt* model, always invoked to explain the formation of a collective colonial odor, interactions between nestmates (e.g., trophallaxis and allogrooming) permit the mixing of individual odors and therefore lead to the formation of the specific colonial odor. The uniformity of this odor is all the more necessary for species with densely populated colonies. In such a system, each member of a colony therefore displays an odor which is representative of the entire colony. Several behavioral studies using recognition tests support this model (Morel and Blum 1988; Crosland 1989a; Provost 1989; Tsuji 1990; Stuart 1988a, 1992). Recent chemical studies have shown that the lipids in the postpharyngeal gland secretion are similar to those found on the cuticle (Bagnères and Morgan 1991; Do Nascimento et al. 1993; Soroker et al. 1995a). In *Cataglyphis niger*, the hydrocarbons stored in this gland are continuously exchanged between nestmates through trophallaxis and allogrooming (Soroker et al. 1994, 1995b) making this gland a *Gestalt* organ in ants (Lenoir et al. in press).

The *Gestalt* model implies a continuous exchange of cues between nestmates. Some studies have shown that the separation of nestmates for a relatively long period disturbs their recognition ability and generates the rejection of individuals previously separated (Kukuk et al. 1977; Jutsum et al. 1979; Crosland 1989b; Provost 1989). This suggests that nestmates must have regular contact to effectively maintain their nestmate tolerance ability. However, regular contact between nestmates throughout the colony is hampered in colonies with satellite nests (called polydomic, see Rosengren and Pamilo 1983). In this type of colonial organization, special behavioral mechanisms allowing contact between individuals of different nests induce the mixing of odors. These behavioral mechanisms consist of the adult transport (e.g., Rosengren 1971; Schmid-Hempel and Schmid-Hempel 1984; Cerdá et al. 1994) or the use of chemical trails connecting the nests (e.g., MacKay and MacKay 1983; O'Neill 1988).

C. iberica is a monogynous and polydomous species. Each colony includes several satellite nests centering around a queenright nest (De Haro and Cerdá 1984). Cerdá et al. (1994) and Dahbi et al. (1997) showed that the frequency of mutual transport between these nests fluctuates seasonally during the active season. Its frequency is high just after hibernation (April), decreases progressively throughout the active period (April-October) and totally disappears during hibernation (November-March). If cues transfer between nestmates occurs in this species, then nest isolation in winter due to the polydomous structure of the colonies would produce a unilateral chemical label within each nest, thereby creating a mosaic of odors throughout the colony's nests. In the present work, we test this hypothesis in *C. iberica* by analyzing the consequences of nest separation for a long period on nestmate recognition and postpharyngeal gland hydrocarbon profiles. We will also examine the effect of hibernation as well as the mixing of individuals after their separation.

Methods

Two *C. iberica* queenless colonies, A and B, composed of three (a_1, a_2 and a_3) and two nests (b_1 and b_2), respectively, were collected at Bellaterra near Barcelona (Spain). Each of these nests included several hundred workers. These colonies were reared in the laboratory under standard conditions (25 °C ± 2 °C, 50% humidity, photoperiod of 10:14 dark/light). Although the influence of environmental factors on nestmate recognition seems to be secondary in this species, all the nests were fed identically with meal worms and a honey-apple mixture and reared in the same nest material to prevent any influence of these factors on recognition cues.

We used colony A to study the consequences of a long period of nest separation on the hydrocarbon profile and interindividual recognition. The effect of hibernation was tested with colony B. All ants belonging to the same nest were marked with the same color-dots to identify their nest origin after reunification. Previous observations showed that this marking technique does not affect ants' behavior.

Ant behaviour was investigated using dyadic encounters taking place in a neutral arena (circular box of 8 cm in diameter, cleaned with alcohol before each encounter). Individuals were changed after each encounter to avoid any ambiguity due to a familiarization effect. Behavioral data were recorded using an event-recorder and results are expressed by the mean (±SE).

Chemical analysis was conducted according to earlier experiments (Dahbi et al. 1996, 1997). We used the postpharyngeal gland (PPG) secretion to avoid contamination from other glandular sources (e.g., Dufour gland), and acetone as solvent since the extracts are identical to those obtained with pentane in *Cataglyphis* ants (authors, unpublished data). The PPGs were individually dissected and immersed for 24 h in 100 µl of acetone. Each extract was then dried under nitrogen and diluted with 50 µl of acetone; 2 µl of the diluted extract were analyzed using gas chromatography on a DELSI 300 with a capillary column (Chrompack CPSIL 5 WCOT, length: 25 m, diameter: 0.22 mm) and a temperature programmed from 100 °C to 280 °C at 3 °C/min. The surface of the chromatogram peaks was determined by an ENICA 21 integrator. We compared the PPG secretion profiles with a factorial analysis of correspondences using the relative proportions of the 24 major peaks of the spectrum (see Table 1). The chemical analysis of PPG secretion resulted in the identification of only hydrocarbons (Dahbi et al. 1996).

Effect of separation on intracolonial recognition

The three nests of colony A (a_1, a_2 and a_3) were maintained apart for 1 year after being excavated and then reunited for 5 months. A behavioral study of interindividual recognition was performed after 12 months of nest separation (periods T_s) and 5 months after their being reunited (period T_r). Three dyadic combinations were possible using the three nests. Each dyadic encounter lasted for 10 min and five replicates were conducted for each type of dyad. Control dyads used workers from the same nest. No aggression appeared and observed interactions essentially consisted of mutual antennations. We therefore took as a unit of measure the frequency and duration of mutual antennations during encounters.

The analysis of the workers' hydrocarbon profiles in each nest was conducted just after field collection (period T_c), during period T_s and during period T_r. For each of the three periods, five indi-

Table 1 Chemical identity of the 24 major substances of the postpharyngeal gland content in *Cataglyphis iberica* workers (*Me* and *DiMe* correspond to monomethyl and dimethyl, respectively). For the complete determination of cuticular hydrocarbons in *C. iberica*, see Dahbi et al. (1996). *Asterisks* mean that differences are significant for each compound between the three nest profiles from colony A, after the separation period (column T_s) and between group profiles from colony B, at the end of hibernation (*EH*) and one month later (*M*). Statistical comparisons were performed using the Kruskal-Wallis rank test

Peak	Chemical	Colony A	Colony B					
		T_s	$b_1 \times b_{2a}$		$b_1 \times b_{2b}$		$b_{2a} \times b_{2b}$	
			EH	M	EH	M	EH	M
P_1	C_{27}							
P_2	11 + 13Me-C_{27}	*	*	–	*	*	–	**
P_3	C_{28}		**	–	–	–	–	–
P_4	C_{29}		**	–	**	–	–	–
P_5	13 + 15Me-C_{29}	**	**	**	**	**	–	**
P_6	9Me-C_{29}		**	–	**	**	–	**
P_7	7Me-C_{29}	**	–	–	–	–	–	*
P_8	5Me-C_{29}		*	–	*	**	–	**
P_9	11, 13DiMe-C_{29}		**	–	–	**	–	**
P_{10}	7, 17 DiMe-C_{29}		–	–	–	**	–	**
P_{11}	3Me-C_{29}		**	–	**	**	–	**
P_{12}	5, 9DiMe-C_{29}		**	–	**	**	–	**
P_{13}	x, y DiMe-C_{29}	*	**	–	**	**	–	**
P_{14}	3, 9DiMe-C_{29}		**	–	**	**	–	**
P_{15}	4Me-C_{30}	**	–	**	*	**	–	**
P_{16}	C_{31}		**	–	**	**	–	**
P_{17}	15Me-C_{31}		**	**	**	**	–	**
P_{18}	9Me-C_{31}	**	**	–	**	**	–	**
P_{19}	7Me-C_{31}	**	**	–	–	**	–	**
P_{20}	5Me-C_{31}	*	**	–	**	**	–	**
P_{21}	11, 15DiMe-C_{31}	*	**	–	**	*	–	*
P_{22}	4, 22DiMe-C_{32}		–	–	–	**	–	**
P_{23}	x, 15DiMe-C_{32}	**	–	–	*	**	–	**
P_{24}	13, 17DiMe-C_{33}		**	–	**	**	–	**

*$P \leq 0.05$, **$P \leq 0.001$

viduals per nest were randomly chosen and their PPG secretion profiles analyzed in order to detect divergence between the profiles of the three nests after their separation.

Effect of hibernation on intracolonial recognition

At the beginning of the hibernation period (November), nest b_2 from colony B was placed in a room where natural conditions of hibernation were reproduced (temperature 10–12 °C, and no food was provided). Nest b_1 was maintained in normal conditions (see below). At the end of hibernation (April), nest b_2 was subdivided into two experimental groups (b_{2a} and b_{2b}) with 120 workers each. Individuals from group b_{2a} were added to nest b_1 whereas individuals from group b_{2b} remained separated but out of hibernation.

Dyadic encounters of 5 min including nest b_1 and groups b_{2a} and b_{2b} were conducted just after the end of hibernation and one month later. We obtained three types of encounters ($b_1 \times b_{2a}$, $b_1 \times b_{2b}$ and $b_{2a} \times b_{2b}$). During each period (the end of hibernation and a month later) 20 replicates were conducted for each type of encounter. We recorded non-aggressive (mutual antennation, submissive posture) and aggressive interactions (only the opening of the mandibles was observed). We calculated the mean aggressive frequency of interactions for each type of encounter, just after hibernation and a month later. This aggressive frequency corresponded to the ratio: frequency of aggressive acts/frequency of total interactions.

We also compared the PPG hydrocarbon profiles of individuals from nest b_1 and from groups b_{2a} and b_{2b}, just after hibernation and a month later. Five individuals per group and period were randomly chosen for this chemical comparison.

Results

Effect of nest separation on intracolonial recognition

The separation of the nests for 12 months did not lead to the appearance of aggressive behaviors between nestmates. The interactions were always limited to mutual antennation. However, this separation clearly increased the duration of the antennal interactions (Table 2). The mean duration per antennal exchange was significantly higher when individuals were previously separated than for control encounters (9.0 ± 0.8 s and 3.7 ± 0.3 s, respectively) ($P < 0.001$). After the three nests were reunited, the duration of antennal interactions returned to values similar to those observed with control dyads (3.2 ± 0.2 s and 3.3 ± 0.4 s, respectively) ($P > 0.05$). However, the separation of ants did not lead to a higher mutual antennation frequency (Table 2). In fact, this frequency remained constant between test and control dyads in the T_s and T_r periods ($P > 0.05$).

The factorial analysis of correspondences was conducted among the three periods T_c (after field collection), T_s (after nests' separation) and T_r (after nest reunification) (Fig. 1). The profiles of the three nests (a_1, a_2 and a_3) differed slightly at period T_c, they diverged

much more after separation (T_s) and were completely similar after reunification (T_r). The analysis also reveals the temporal evolution of the colony profile among the three periods. The characteristic colonial profile at T_c was different from the profile at T_r, with an intermediate situation at T_s.

The factorial analysis of correspondences compares the hydrocarbon profiles of the different nests as a whole without precisely defining the number and the nature of substances involved in divergence. A comparison of the relative proportions of the different peaks between individuals of the three nests at T_c, T_s and T_r (Table 1), confirms this profile divergence between the three nests after separation and determines the "plastic" peaks ($P < 0.05$). The column for Colony A shows the high number of peaks which vary significantly between individuals of the three nests after separation. This variation concerns 10 hydrocarbons of 24, essentially monomethylalkanes, especially 13 + 15MeC_{29}, 7MeC_{29}, 4MeC_{30}, 15MeC_{31} and 9MeC_{31}.

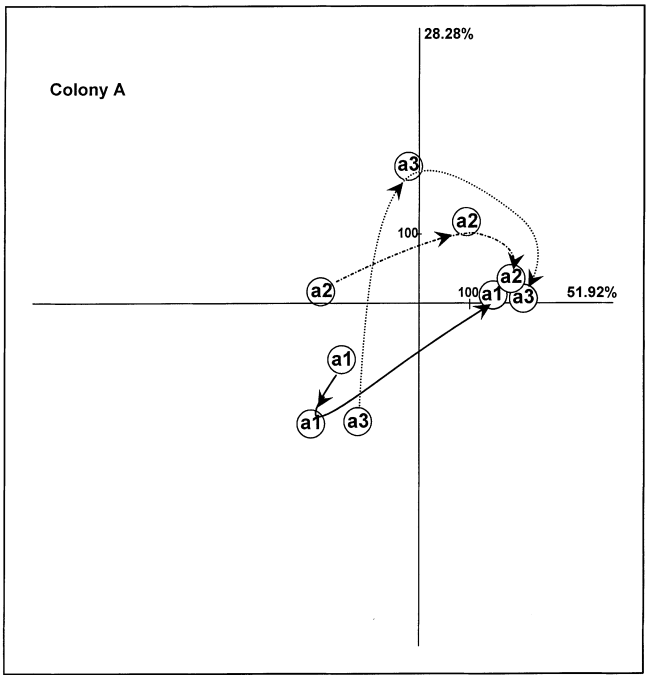

Fig. 1 Factorial analysis of correspondences performed on the three nests of colony A at T_c, T_s and T_r. Each nest profile is represented by the mean point of its individual profiles. For each nest, *arrows* indicate the temporal change of profile in the bidimensional space (example: $a_1 \rightarrow a_1 \rightarrow a_1$ concerns the profile of the nest a_1 at T_c, T_s and T_r, respectively)

Effect of hibernation on intracolonial recognition

Encounters between ants resulted in amicable as well as aggressive interactions. The latter, which consisted only in the opening of the mandibles, essentially appeared between separated nestmates (Table 3). In fact, at the end of hibernation, aggression frequencies during $b_1 \times b_{2a}$ and $b_1 \times b_{2b}$ encounters were significantly higher than the aggression frequency during $b_{2a} \times b_{2b}$ encounters ($P < 0.001$). However, 1 month after the cohabitation between b_1 and b_{2a} individuals, the aggression frequency in the dyads $b_1 \times b_{2a}$ became lower than aggression scores recorded in dyads $b_1 \times b_{2b}$ and $b_{2a} \times b_{2b}$ ($P < 0.001$). The evolution of the aggression frequency between the end of hibernation and one month later reveals a decrease in aggressiveness for dyads $b_1 \times b_{2a}$ and $b_1 \times b_{2b}$ and a slight increase in the aggressive interactions for dyads $b_{2a} \times b_{2b}$.

The factorial analysis of correspondences (Fig. 2) shows that after hibernation, b_{2a} and b_{2b} profiles were related but clearly different from the profile of nest b_1. This situation changes one month later, essentially for b_{2a} and b_{2b} individuals. The cohabitation of b_{2a} individuals inside nest b_1 induced a clear convergence of their hydrocarbon profile with that of b_1 workers. The profile of b_{2b} workers also changed after the end of

Table 2 Mean durations (sec.) (±SE) of one antennal interaction and mean antennal frequencies (±SE) during one dyadic encounter (10 min). Data were recorded at T_s (after separation) and T_r (after reunification). Test and control dyads mean that the dyadic partners came from different nests and from the same nest, respectively

Colony A	Antennal durations			Antennal frequencies		
	T_s	T_r	Student *t*-test	T_s	T_r	Student *t*-test
Test dyads (n = 15)	9.0 ± 0.8	3.2 ± 0.2	$P < 0.001$	25.1 ± 2.0	25.5 ± 1.6	NS
Control dyads (n = 15)	3.7 ± 0.3	3.3 ± 0.4	NS	21.7 ± 2.1	22.9 ± 1.1	NS
Student *t*-test	$P < 0.001$	NS		NS	NS	

Table 3 Mean aggression frequency (±SE) calculated for each type of dyad for both observation periods: at the end of hibernation (*EH*) and 1 month later (*M*). For each period (columns), significant differences are shown by different letters (Student *t*-test, $P < 0.05$)

Colony B	EH	M	Student *t*-test
$b_1 \times b_{2a}$ (n = 20)	0.57 ± 0.03 a	0.14 ± 0.01 a	$P < 0.001$
$b_1 \times b_{2b}$ (n = 20)	0.59 ± 0.05 a	0.33 ± 0.04 b	$P < 0.001$
$b_{2a} \times b_{2b}$ (n = 20)	0.05 ± 0.02 b	0.23 ± 0.02 b	$P < 0.001$

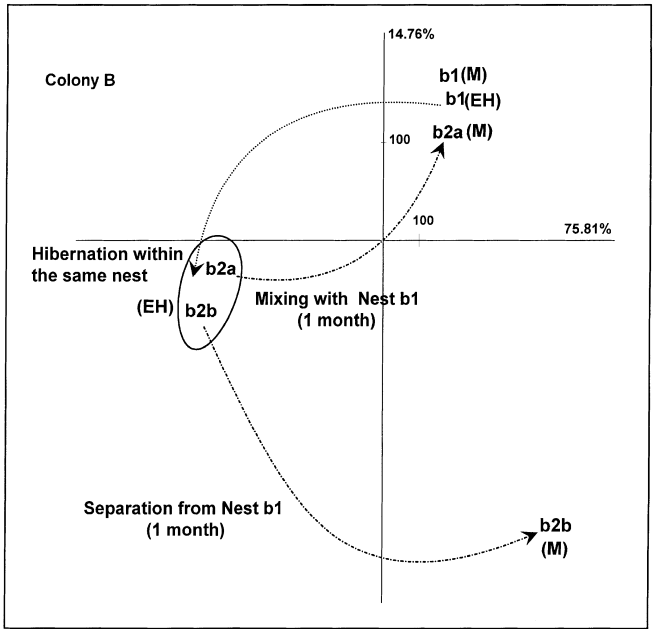

Fig. 2 Factorial analysis of correspondences performed on groups from colony B at the end of hibernation (*EH*) and 1 month later (*M*). Each group profile is represented by the mean point of its individual profiles. *Arrows* indicate the evolution of each group profile in the bidimensional space (b_1 is the nest kept at room temperature and $b_{2a} + b_{2b}$ the groups placed at hibernation temperature during the hibernation period within the same nest)

hibernation without converging with the b_1 profile. These results are confirmed by the number of divergent peaks between b_1, b_{2a} and b_{2b} profiles for each of the two periods (Table 1, column Colony B). After cohabitation between b_{2a} and b_1 individuals, this number decreased. However, it remained high for b_{2b} individuals that remained isolated from nest b_1. In contrast, one month after the end of hibernation, most of the peaks diverge between b_{2a} and b_{2b} individuals. It is noteworthy that the hibernation effect on hydrocarbon profiles concerns all chemical classes (*n*-alkanes, mono- and dimethylalkanes) ($P < 0.05$).

Discussion

Numerous behavioral studies conducted on ants have used the technique of splitting colonies to highlight some of the mechanisms involved in nestmate recognition and the elaboration of a specific colony odor (see Introduction). In most of these experiments, however, the queen was kept in one half of the colony. The behavioral alteration in intracolonial recognition observed by these authors was generally explained by the queen's effect on the workers' odor. Moreover, environmental influences such as food and the presence of the queen on nestmate recognition cues have been investigated in several studies (Jutsum et al. 1979; Carlin and Hölldobler 1983, 1986; Obin and Vander Meer 1988; Bennett 1989; Crosland 1989c, 1990). However, the change in the odor of *C. iberica* workers seems to be endogenous since our experimental groups were all queenless and fed identically. This lends credence to the idea that the acquisition of the group label originates exclusively in the chemical cues transferred between individuals within the same group. Each group elaborates a *Gestalt* odor representing its individual characteristics and diverging from those of other groups. If there were no such transfers, the profiles would change in the same manner during the separation. However, we can not exclude the possibility that isolation also induced some hormonal perturbations which in turn affected individual odors.

Despite a long period of separation between workers of *C. iberica*, nestmate recognition remained effective as was observed in *Formica fusca* (Wallis 1962). Nevertheless, nestmate separation induced hydrocarbon profile divergence as well as behavioral changes. Mutual antennation, which mediates interindividual discrimination, increased in duration after individuals had been separated. This behavioral modification is associated with chemical changes in hydrocarbon profiles. Encounters between hibernating and non-hibernating individuals induced more obvious aggressive interactions. However, these interactions were limited to the opening of the mandibles and never reached the intercolonial level of hostility observed in this species. In *C. iberica*, allocolonial encounters in a similar dyadic situation induce injuries and death (Dahbi et al. 1996). The low-level hostilities observed after separation suggest the emergence of minor differences between the odors of separated nestmate groups, which did not reach the level of allocolonial odor disparity. This was corroborated by the analysis of the PPG hydrocarbon profiles, which revealed a slight divergence in profiles due to the separation. This divergence was stronger between individuals who hibernated than those who remained under normal conditions, which could explain the occurrence of some aggressive behaviors. The higher degree of divergence following hibernation could be explained by the physical separation of nestmates combined with physiological modifications in hibernating ants. The link between behavior and hydrocarbon profiles was again demonstrated when previously separated individuals were again in contact. After contact, antennations decreased and aggressive interactions disappeared. The concomitant decrease in disparities between hydrocarbon profiles suggests that these are involved in the behavioral alterations observed. Provost (1989) also showed in *Leptothorax lichtensteini* that long antennations and rare aggressive incidents occurred after two halves of a colony previously separated for 4 months were merged. In *Camponotus vagus*, modification of cuticular hydrocarbon profile by topical application of 9-(Z) tricosene induces an increase in antennal duration towards treated nestmates (Meskali et al. 1995).

Group size can also influence the evolution of respective profiles during the formation of the *Gestalt* odor. Carlin and Hölldobler (1983) and Stuart (1988b)

speculated that when two or more groups are joined together, and the *Gestalt* odor is effective and uniformly widespread among all individuals, then the larger group will make a greater contribution to the new *Gestalt* odor. This seems to be the case in *C. iberica*. After reunification, the profile of the small group b_{2a} (120 workers) changed unilaterally, converging toward the profile of nest b_1 (several hundred workers), probably because of its small size relative to nest b_1. All nestmates may contribute equally to the elaboration of the colonial *Gestalt* odor, leading to a mean odor of all members which is therefore more representative of the larger group.

Workers reunited after several months of separation engaged in more trophallactic exchanges and were not aggressive towards each other (authors, unpublished work). Since trophallaxis constitutes the major means by which nestmates exchange their recognition cues (Soroker et al. 1994, 1995b), this suggests that when joined, previously separated nestmates can perceive divergent odors and preferentially exchange their recognition cues, mainly by trophallaxis, to obtain a uniform recognition odor. During hibernation the complete isolation of nests in combination with possible endogenous modifications would induce odor divergence between homocolonial nests. This is reflected by the slight divergence between the three nests in period T_c, since these nests were collected in April, corresponding to the end of hibernation. The high frequency of adult transport results in mixing of nestmates and may therefore increase the uniformity of colony odor (Dahbi et al. 1997). As mutual transport affects only a fraction of the colony (Cerdá and Retana 1992), we assume that chemical cues can move between nests through these transportee workers to generate an efficient distribution system among all polydomous colony members.

In a polydomous species like *C. iberica*, the transfer of recognition cues between nestmates seems to be even more necessary in generating an unambiguous colonial odor. In this species, nests are relatively densely packed but colonies are very closed (Dahbi et al. 1996). An efficient *Gestalt* odor among satellite nests is then needed to avoid any ambiguity in their recognition system. This marked social closure in *C. iberica* may be an adaptive response to the high scarcity of food resources which are spatially and temporally unpredictable. Social closure may constitute a strategy against food robbing between allocolonial nests. In *C. iberica*, there is no colonial territory and competing foreign nests can be spatially very close. Since this may favor intercolonial intrusions, a uniform collective odor among all satellite nests allowing workers to discriminate intruders without ambiguity is then required. The persistence of a mosaic of odors among satellite nests of each colony would reduce the recognition efficiency of neighboring foreign competitors.

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