Adult transport in the ant *Cataglyphis iberica*: a means to maintain a uniform colonial odour in a species with multiple nests

A. DAHBI,[1] X. CERDÁ[2] A. HEFETZ[1,3] and A. LENOIR[4]
[1]Laboratoire d'Ethologie Expérimentale et Comparée, URA 2214, Université Paris Nord, Villetaneuse, France,
[2]Unidad de Ecología Evolutiva, Estación Biológica de Doñana, CSIC, Sevilla, Spain,
[3]Department of Zoology, George S. Wise Faculty of Life Science, Tel Aviv University, Ramat Aviv, Tel Aviv, Israel, and
[4]Laboratoire d'Ethologie et Pharmacologie du Comportement, Faculté des Sciences et Techniques, Tours, France

Abstract. Societies of the ant *Cataglyphis iberica* (Hymenoptera, Formicidae) comprise several satellite queenless nests around a queenright nest. During spring, at the end of hibernation, the incidence of adult transport between these nests is high, but it decreases during summer. Quantitative analyses of the contents of postpharyngeal glands of transporter and transportee ants reveal the amounts of hydrocarbons to be lower in the latter, indicating that these ants are generally younger. Moreover, the more diverse composition of the transportees' secretion may reflect their individual makeup. Transporters, in contrast, maintained a uniform colony odour through trophallactic exchanges before entering hibernation. The odour disparity between the transportees and the general colony odour may stimulate the transporters to bear them to the nest containing the queen where they can obtain the colony odour via trophallaxis. The intense traffic between satellite nests in the spring may thus be the means by which a uniform colonial odour is regained after hibernation. Adult transport seems also to be necessary since the young transportee ants are not able to orient themselves and find the other nests.

Key words. *Cataglyphis iberica*, polydomy, adult carrying, hydrocarbon profiles, 'gestalt' odour.

Introduction

Social insects, particularly ants, are notable for their ability to discriminate nestmates from alien individuals. This capacity enables them to maintain the cohesion of the colony, yet protect it from conspecific intruders. Discrimination is achieved through the perception of chemical signals that reside on the cuticular surface and constitute the colonial odour (Hölldobler & Michener, 1980). Among these chemicals, hydrocarbons are believed by many authors to provide the recognition signals (Bonavita *et al.*, 1987; Morel *et al.*, 1988; Henderson *et al.*, 1990; Nowbahari *et al.*, 1990). They are species specific and vary quantitatively between members of different colonies, fulfilling the requirements for a colonial odour.

Correspondence: Dr A. Dahbi, LEEC Laboratoire d'Ethologie Expérimentale et Comparée, URA 2214, Université Paris Nord, Av. J.-B. Clément, 93430 Villetaneuse, France.

According to Crozier & Dix (1979), colonial recognition odour constitutes a 'gestalt' of the odours of all members of the nest and is acquired by special transfer mechanisms. The transfer of recognition cues between members of the colony was inferred from behavioural data, i.e. the transfer of recognition cues from queen to worker in *Camponotus* (Carlin & Hölldobler, 1983) or from nurse ants to callows (Morel & Blum, 1988). Recent biochemical studies have confirmed such a transfer, and identified the postpharyngeal gland as the 'gestalt' organ. A uniform colonial odour is attained by frequent exchange of postpharyngeal glandular secretion between nestmates, mostly via trophallaxis but also through allogrooming (Hefetz *et al.*, 1992; Soroker *et al.*, 1994, 1995a; Vienne *et al.*, 1995). Hydrocarbon transfer between individual cuticular surfaces was also observed in *Camponotus vagus* (Meskali *et al.*, 1995). Thus, the odour of a colony is not rigidly constant, but rather dynamic and influenced by the individual composition of the nest at a given time. Temporal changes in cuticular hydrocarbons were demonstrated for adults in the fire ant *Solenopsis invicta* (Vander Meer *et al.*, 1989), in

Leptothorax lichtensteini (Provost *et al.*, 1993) and for callows in *Camponotus* (Morel *et al.*, 1988; Bonavita-Cougourdan *et al.*, 1990).

Some ant species tend to enlarge their foraging area by creating multiple nests, making polydomous colonies (Hölldobler & Wilson, 1990; Bourke & Franks, 1995). Polydomy may be linked with a high nest density which constrains colonies to have a efficient 'gestalt' odour and to avoid ambiguity in their recognition system. The maintenance of a uniform colony odour in such species may require a constant movement of workers between satellite nests and extensive exchanges of glandular secretions, in order to avoid unilateral changes in odour composition.

The phenomenon of worker exchanges between nests in polydomous ants has been studied in many species, mainly of the *Formica* genus, in which this traffic is performed simply by moving along trails (Pisarski, 1972; Czechowski, 1975; MacKay & MacKay, 1983; O'Neill, 1988; Henderson & Jeanne, 1992) or by adult carrying (Rosengren, 1971; Ito & Imamura, 1974; Imamura, 1978; Rosengren & Pamilo, 1983). In these species, adult exchange is seasonal, reaching a maximum in spring (budding to the secondary nests) and autumn (regrouping to the main nest). Adult carrying is also frequent in *Cataglyphis* ants, where it was observed in *C.bicolor* (Schmid-Hempel & Schmid-Hempel, 1984) and in *C.iberica* (Cerdá & Retana, 1992; Cerdá *et al.*, 1994). Earlier studies (Økland, 1934; Kneitz, 1964; in Hölldobler & Wilson, 1990) have already suggested that adult transport may serve as an important means of colony integration. The present paper concerns *C.iberica*. Unlike *Formica* species, this species undergoes winter hibernation in separate nests. Its seasonal activity starts towards the end of March/beginning of April and continues until October. It has only one peak of transport in spring (Cerdá *et al.*, 1994).

In this paper we characterize the glandular constituents of transporter and transportee ants as well as their effect on the maintenance of a uniform colonial odour. A uniform odour, including all satellite nests, is necessary because nests of neighbouring *C.iberica* colonies are spatially close and conspecific intruders are not tolerated (Dahbi *et al.*, 1996).

Material and Methods

Field observations of transport activity. Transport activity was observed in three field colonies of *C.iberica* (comprised of four to seven, three to five, and seven to nine satellite nests respectively, depending upon the period of the year), situated near the UAB campus (Universitat Autònoma de Barcelona, Bellaterra, Spain) where a high density of colonies occurs (15–20 colonies/ha with 50–150 satellite nests/ha). Transport activity was monitored monthly during the ants daily activity period (09.00–19.00 hours). The two following variables were measured for all the satellite nests of the three colonies: adult transport activity = T = the sum of the numbers of workers that entered or left a nest carrying a nestmate each time at 12.30, 13.30, 14.30 and 15.30 hours during 15 min; foraging activity = F = the sum of the numbers of workers that entered or left a nest without a transportee ant at 13.00, 14.00 and 15.00 hours, each time during 5 min. F was multiplied by 4 to extrapolate the data for 1 h.

From these two variables the ratio of transport activity to foraging activity = $R_{T/F}$ = T/F was calculated. For the queenless nests of one colony we calculated the expected values of transport per hour and per nest, according with the formula $(\Sigma T_i)/n - 1$, where T_i is the total activity (entries or exits) counted during 1 h for the nest *i*, and *n* is the number of nests in colony. These 'expected queenless values' were compared with the observed queenright value (the same activity counted in the queenright nest during the same period) by means of a Wilcoxon matched pairs test.

We indexed transport and foraging activities to test whether changes in transport activity are only a function of colony activity level or if these parameters vary independently.

Chemical analyses. Cuticular and postpharyngeal hydrocarbons of *C.iberica* have been identified previously by mass spectrometry (Dahbi *et al.*, 1996). Twenty-four pairs of ants, transporter and transportee, originated from two different colonies (A and B, sixteen and eight pairs respectively), were collected in May during adult carrying for qualitative and quantitative chemical analyses of their postpharyngeal gland secretions. The ants were killed by freezing immediately following their capture, dissected under water and their glands were extracted in acetone for 24 h. The extracts were dried under nitrogen, then redissolved in 50 μl acetone of which 2 μl were injected to the gas chromatograph (DELSI 300). The samples were run on a CPSIL 5 WCOT capillary column (25 m × 0.22 mm) temperature programmed from 100 to 280°C at 3°C/min. Quantification was by peak integration using an Enica 21 integrator with the following formula:

$$W = TPS \times \frac{W_{(es)}}{S_{(es)}} \times 25$$

where W = weight of the postpharyngeal gland secretion in μg; TPS = total peak area of the 2 μl sample; $W_{(es)}$ = weight in μg of the external standard (octadecane); $S_{(es)}$ = peak area of the external standard; and 25 = the dilution factor.

The similarity of the hydrocarbon profiles of sixteen of these pairs (eight pairs from each colony) was further studied by cluster analysis of cases. The analysis was based on the relative intensity of fifteen major peaks. We also compared the homogeneity of profiles for transporters and transportees, using amalgamation distances, which are the geometrical distances between individuals in a multidimensional space, and are used for the cluster construction. The profile homogeneity traduces the similarity between individual profiles.

Results

Field observations showed that adult carrying activities of *Cataglyphis iberica* were not uniform throughout the activity season (Table 1) but that, during April and May, many adult transports occurred. Thereafter it declines slowly to reach a minimal level towards the end of the activity season (September). This seasonal variability is emphasized when comparing the two common external activities: adult transport activity and foraging. Following hibernation, the ratio of adult transport to foraging ($R_{T/F}$) is maximum. This high ratio existing in April and May decreases as summer activity progresses (until August), this being

Table 1. Seasonal activities of adult transport and foraging of *Cataglyphis iberica*. For definitions of transport activity (*T*), foraging activity (*F*) and the ratio $R_{T/F}$, see Methods. Mean values (±SE) followed by different letters are significantly different (Fisher's PLSD test, $P < 0.05$).

Month	T	F	$R_{T/F}$	n
April	20.6 ± 8.0 (a, b)	114.3 ± 28.4 (a)	0.15 ± 0.03 (a)	7
May	24.6 ± 10.7 (a)	252.6 ± 23.2 (b)	0.09 ± 0.03 (a)	7
June	10.8 ± 1.6 (a, b)	180.0 ± 24.7 (c)	0.06 ± 0.01 (a)	7
July	8.0 ± 1.3 (b, c)	187.6 ± 12.7 (c)	0.04 ± 0.02 (a)	11
August	8.2 ± 9.2 (b, c)	145.3 ± 13.1 (a, c)	0.05 ± 0.01 (a)	14
September	4.7 ± 2.1 (c)	97.9 ± 16.2 (a, d)	0.10 ± 0.07 (a)	12

due to a significant decrease in adult transport rather than higher foraging activity. In September the ratio $R_{T/F}$ was high again, this late increase resulting from a decrease in foraging activity (Table 1).

There was also a spatial variability in the intensity of transport between the satellite nests. The mean (±SE) transport activity per hour for entrances was 13.1 ± 2.3 and 3.4 ± 0.9 for queenright and queenless nests, respectively (Wilcoxon test, $P < 0.001$, $n = 18$). A statistical difference was also found for the exit transports which were more frequent in the queenright (8.7 ± 1.7) than the queenless nests (4.4 ± 0.6, Wilcoxon test, $P = 0.02$, $n = 18$). This may indicate a more important role for the queen among the satellite nests.

The content of the individual postpharyngeal gland secretions extracted from the twenty-four pairs of transporter–transportee workers, belonging to the two colonies, was quantified by gas chromatography (Table 2). Taking into account the ants from both colonies (A and B), there were no differences in the average amounts of secretion between the ants (all workers or transporters or transportees) of the two colonies (Mann-Whitney U-test, $P > 0.05$). In contrast, clumping of the ants according to their behaviour (transporters v transportees) revealed that in nest A the average amount of secretion in the transporter ants was significantly larger than that of the transportee of the same nest (1.11 v 0.77μg, Wilcoxon test, $P = 0.029$). In nest B the same

tendency appeared but was not statistically different, probably due to the low number of pairs analysed for this nest (Table 2). Supporting these findings was a paired comparison of the amount of secretion present in the gland between transporter–transportee ants: in seventeen out of the twenty-four pairs tested (twelve out of sixteen pairs and five out of eight pairs for colonies A and B respectively), the transporter ants had higher quantities of secretion than the ants they carried (Fig. 1).

The next questions were whether the secretion is colony specific, and whether the transporter ants differ from transportees within each colony. To assess the degree of similarity in the glandular compositions between the ants of the different colonies and the different roles in adult carrying, we performed a cluster analyses of cases based on fifteen major hydrocarbons present in the secretion. Fig. 2 depicts the dendrogram obtained by cluster analysis of ants from both nests. From the clustering it is evident that ants of each colony carry a specific profile. This segregation according to colony origin is significant when we compare the amalgamation distances before clustering, between the patterns of ants within colony (5.78 for A and 7.99 for B) to the distances between the pattern of ants from different colonies (9.65 for A v B, Mann-Whitney U-test, $P < 0.001$).

When we examined the clustering within each nest, however, the transporter ants could be discriminated from the transportees. For colony A, the amalgamation distances were 4.25 within transporters and 6.70 within transportees (Mann-Whitney U-test, $P < 0.05$). For colony B, the discrimination between the two groups was less evident: 6.09 and 8.27 within transporters and within transportees, respectively (Mann-Whitney U-test, $P > 0.05$). This lack of statistical significance is probably due to a greater variability in colony B. Furthermore, Factorial analyses of correspondences performed on these two nests on the basis of the patterns of their postpharyngeal gland secretion revealed that the transporter ants were much more homogenous than the transportees (Fig. 3).

Discussion

Adult transport constitutes an important component in the social behaviour of *C.iberica*. Transporter ants form a special

Table 2. Quantitative analyses of the postpharyngeal glands of pairs of transporter–transportee ants from two colonies (A; B) of *Cataglyphis iberica*. Samples were run by gas chromatography, and the amount of secretion (mean ± SE) determined by peak integration. For detailed calculations see Methods. The differences between either workers, or transporters, or transportees from the two different colonies were statistically appreciated by a Mann-Whitney U-test. The differences within a nest between transporters and transportees were appreciated by Wilcoxon matched pairs.

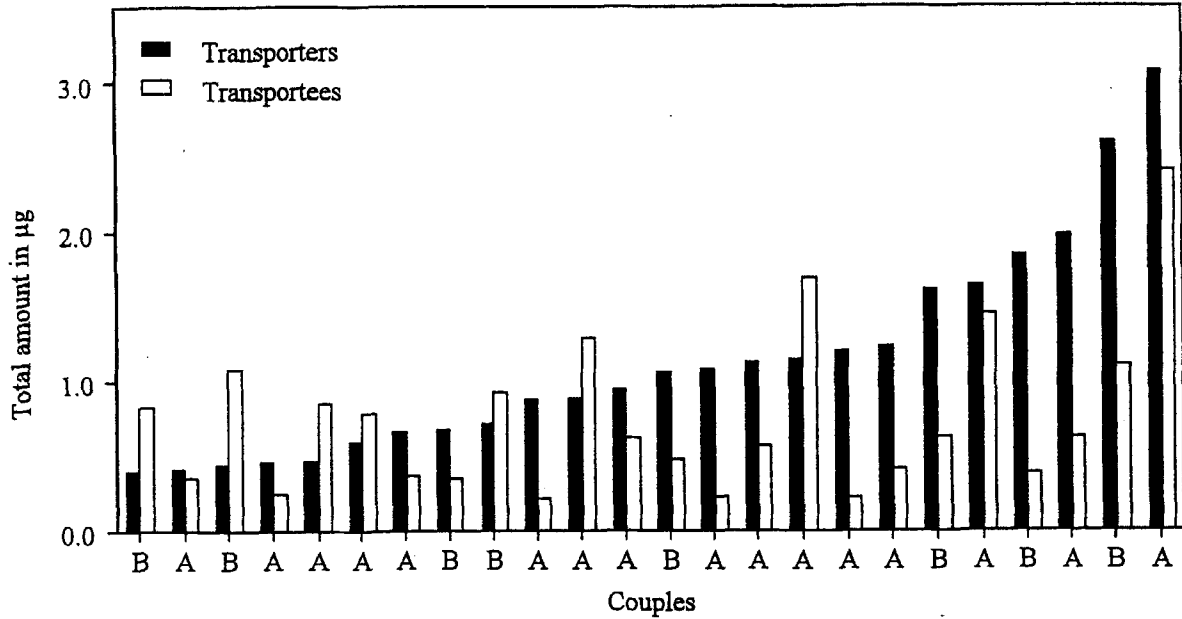| Workers category	Amounts of secretion in the postpharyngeal glands (μg)		P (Mann-Whitney) colony A/colony B
	Colony A	Colony B	
All workers (n = 48)	0.94 ± 0.12	0.95 ± 0.15	>0.05
Transporters (n = 24)	1.11 ± 0.17	1.17 ± 0.28	>0.05
Transportees (n = 24)	0.77 ± 0.16	0.72 ± 0.11	>0.05
P (Wilcoxon) transporters/ transportees	0.029	0.207	

Fig. 1. Total amounts in μg of the postpharyngeal gland content of pairs of transporter and transportee *Cataglyphis iberica* ants collected during adult carrying in the field. A and B indicate the colony origin of couples.
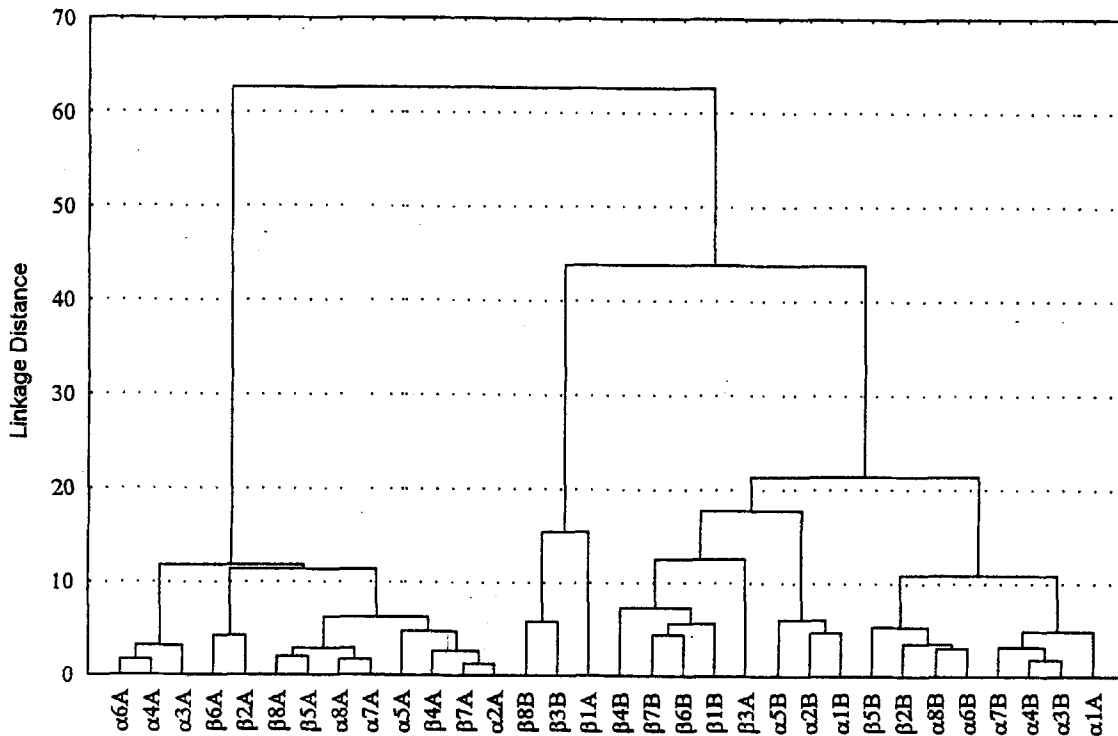

Fig. 2. Cluster analysis, based on the postpharyngeal hydrocarbon profiles of transporter and transportee individuals from two colonies of *Cataglyphis iberica*. Individuals are coded as follows: α1A, transporter individual 1 from the colony A; β1A, transportee individual 1 from colony A. Transporter and transportee having the same number were collected as pairs during adult transport in the field.

behavioural subcaste composed of old workers, and can be defined as an intermediate behavioural stage between intranidal workers and foragers. Transportees, on the other hand, are mostly young workers that do not form a particular subcaste but belong

to all other behavioural subcastes that characterize the colony (Cerdá & Retana, 1992).

The two categories of workers seem to differ in the quantity of secretion present in the postpharyngeal gland. On average,
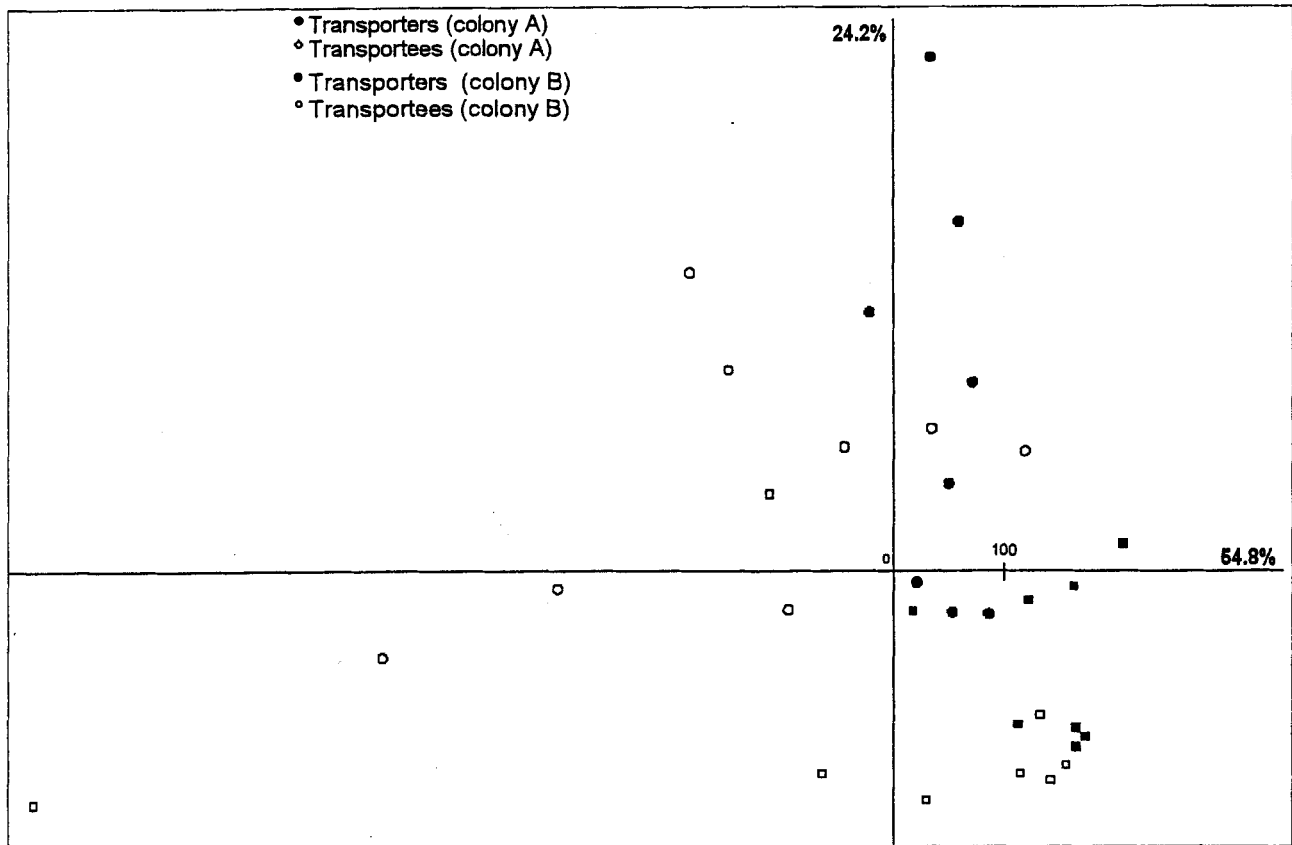
Fig. 3. Factorial analysis of correspondences based on postpharyngeal hydrocarbon profiles for *Cataglyphis iberica* transporters and transportees from colonies A and B.

transporters had larger amounts of secretion than the transportees. First, though this fact was not significant for one of the two tested colonies, the tendency to higher amounts of secretion in the transporter ants was apparent. Secondly, in the majority of the pairs collected in the field during adult transport, the amount of secretion in the transporters was greater than that in the transportees. The lesser amounts in transportee ants indicate that these ants are probably younger. Indeed, in *C.iberica* (Dahbi *et al.*, unpublished data), as in *C.niger* (Soroker *et al.*, 1995b), callow workers have very small amounts of secretion in their postpharyngeal gland in the first days post-eclosion. This quantity increases thereafter for about 10 days until it reaches the average amounts present in adult mature workers.

Nests of *C.iberica* contain cocoons even in mid September, just before they begin hibernation (Cerdá, 1989), so callow workers emerging at that time enter hibernation directly and do not manage to accumulate large quantities of hydrocarbons in their postpharyngeal gland. During hibernation the workers clump into the terminal cell of the nest and become totally inactive including a cessation of trophallactic exchanges and allogrooming (Cerdá & Dahbi, personal observations). Therefore workers that enter hibernation as callows without having had the opportunity to exchange recognition cues, keep their individual composition of the postpharyngeal gland secretion. If the callow workers do not exchange recognition cues with mature nestmates, the composition of their postpharyngeal secretion may

reflect their interindividual variability. This explains the higher degree of heterogeneity exhibited by transportees secretory composition as compared with other older workers that have already acquired the colony odour. It would thus appear that in a hibernating satellite nest two groups of workers exist: older workers possessing large quantities and homogenous postpharyngeal gland secretion, and younger workers with smaller amounts of heterogenous secretion. At the end of hibernation these workers can be still considered as 'physiological callow', and furthermore distinguishable from the older workers that reside in the same satellite nest.

Disparity in the recognition signals may explain the high frequencies of adult transport in early spring. Very young ants which have never left their native nest may have difficulty in finding the position of other satellite nests and therefore have to be guided there. In the absence of chemical trails, naive *C.iberica* guidance is accomplished by adult transport. Adult transport in *Formica truncorum* described by Rosengren & Pamilo (1983) could also be explained in the same way. In the summer a polydomous *Formica* society inhabits fifty to sixty nests and 60% of those nests are deserted in autumn; young workers which are transported to hibernation nests, are probably not able to orient outside. In *C.iberica*, young workers are apparently recognized by their hydrocarbon profile that is distinct from that of older workers comprising the transporter subcaste. These differences in chemical composition are not as large as the

differences between two heterocolonial ants, but large enough to be perceived by the transporter ants. Thus they do not provoke aggression between ants, but induce adult transport. This phenomenon was also reported by Bonavita-Cougourdan *et al.* (1990) for *Camponotus vagus* where young ants found in the foraging arena are retrieved into the nest. Furthermore, social carrying occurs during colony emigration (e.g. in *Cataglyphis bicolor*) (Harkness, 1977). This kind of transport could have an odour basis to allow transporters to discriminate young workers, which are unable to orient themselves into the new site.

Adult carrying continues, albeit to a lesser extent, throughout the season. It is less pronounced since callow workers emerging during the activity season can exchange recognition signals with ants that move frequently between satellite nests. These ants evidently exchanged recognition signals with many adult members of the colony and possess the colonial odour. Exchanges between young workers and older workers tend to minimize the differences in recognition signals between these two categories of ants and lower the probability of adult transport. The transport activity yet exhibited during all the activity season serves to guide interior ants to other nests, what enhances the acquisition of a uniform colonial odour.

It seems necessary for a species like *C.iberica*, whose colonies and nests are relatively packed, to develop an efficient strategy like adult carrying, which ensure to colonies an efficient 'gestalt' odour. We have demonstrated for this species that the age polyethism known for the adult carrying (transporters older and transportees younger workers) has a pheromonal basis. It is interesting to note that most of the transport activity occurred around the nest that contained the queen. Since *C.iberica* is monogynous, the queen may have an impact on the nature of the colonial label (see for example *C.floridanus*; Carlin & Hölldobler, 1983). It is therefore probable that transport of 'physiological callow' ants is directed preferentially towards queen nests for acquisition of the colony odour. Furthermore, in a polycalic species like *C.iberica* in which workers occupy other satellite nests it is important that they be exposed to their queen from time to time in order to maintain social integration. This is especially true for the workers that emerge in a satellite nest just before hibernation and have never been exposed to their queen.

Acknowledgments

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