Comparative dynamics of gestalt odour formation in two ant species *Camponotus fellah* and *Aphaenogaster senilis* (Hymenoptera: Formicidae)

ALAIN LENOIR *[1], ABRAHAM HEFETZ†, TOVIT SIMON† & VICTORIA SOROKER†[1]

*IRBI – CNRS UMR 6035, Université François Rabelais, Faculté des Sciences et Techniques, Tours, France and †Department of Zoology, Tel Aviv University, Ramat Aviv, Israel

Abstract. Ant colonies experience continuous shifts in worker populations, which may affect odour composition in the nest. A major question regarding the dynamics of gestalt formation is that of the speed at which the scent of a new individual will be incorporated into the gestalt. It is predicted from the gestalt model of colony odour that workers have to exchange recognition cues continuously to maintain themselves within the gestalt and become well integrated within their colony. Using radioactive tracers the rates of transfer were measured between a labelled donor ant and one or 10 recipient ants, as a close approximation to the within-nest situation. The labelled hydrocarbons were first transferred to a small number of individuals and progressively to all the individuals of the group so that the distribution of hydrocarbon transfer rate approached a normal distribution. Furthermore, in *Camponotus fellah* Dalla Torre, which performs trophallaxis, homogeneity was reached more rapidly than in *Aphaenogaster senilis* Mayr, which does not show this behaviour. In the latter species, the gestalt seems to be maintained mainly by allogrooming. These experiments were accompanied by behavioural observations to ascertain the respective importance of trophallaxis and allogrooming in the behavioural time-budget of the ants. In *A. senilis*, allogrooming was more frequent than in ants that trophallax, which corroborates the role of allogrooming in the establishment of the gestalt in this species.

Key words. Allogrooming, *Aphaenogaster senilis*, *Camponotus fellah*, gestalt odour, hydrocarbons, postpharyngeal gland, trophallaxis.

Introduction

Chemical cue-mediated nestmate recognition is one of the major characteristics of social insects. There are two basic models for the projection of colony identity: the individualistic model, where each member of the colony bears its genetically determined odour and therefore each member of the colony is individually recognized; and the gestalt model, as proposed for populous colonies in which all the individuals within the colony share their recognition cues to form a 'gestalt colony odour' (Crozier & Dix, 1979; Crozier, 1987). Multiple correlative studies have suggested that, at least in ants and wasps, cuticular substances constitute signals of colonial identity (reviewed in Lorenzi *et al.*, 1996; Singer, 1998; Vander Meer & Morel, 1998; Lenoir *et al.*, 1999). Recent experiments with *Cataglyphis niger* and *Iridomyrmex purpureus* indicate that only the hydrocarbon fraction of the cuticular lipids are needed for nestmate recognition (Lahav *et al.*, 1999; Thomas *et al.*, 1999). It was also demonstrated that the postpharyngeal gland (PPG), a gland unique to the Formicidae, constitutes a reservoir of the colonial odour (Soroker *et al.*, 1994; Hefetz *et al.*, 1996).

We predict from the gestalt model that workers have to exchange hydrocarbons continuously to maintain themselves within the gestalt. Several studies have tested this hypothesis using chemical analyses of members from split colonies or of individually isolated workers, clearly supporting the existence

Correspondence: A. Lenoir, IRBI – CNRS UMR 6035, Université François Rabelais, Faculté des Sciences et Techniques, Parc de Grandmont, 37200 Tours, France. E-mail: lenoir@univ-tours.fr

[1]Present address: Department of Entomology, Institute of Plant Protection, Agricultural Research Organization The Volcani Center, Bet-Dagan, Israel.

of a gestalt colony odour (Dahbi *et al*., 1999; Boulay *et al*., 2000a; Lenoir *et al*., 2001). They also confirmed the prediction that the individual's hydrocarbon composition is dynamic, with workers continuously exchanging hydrocarbons.

Transfer of chemical cues between individuals can be mediated by three modalities: trophallaxis, allogrooming, and other physical contact. In the formicine ants, where trophallaxis is very frequent, this behaviour constitutes the major modality for sharing colonial odour (*C. niger*, *C. iberica* and *Camponotus fellah* Dalla Torre; Soroker *et al*., 1995; Dahbi *et al*., 1999; Boulay *et al*., 2000a). On the other hand, allogrooming and other physical contact are the means by which species that do not perform trophallaxis can exchange body odours. In the ponerine ant *Pachycondyla apicalis* it was shown through the use of radioactive tracers and behavioural observation that odour transfer is mediated via other physical contact. This mode of transfer seems to be sufficient for a gestalt formation in this species, which has small colonies of fewer than 100 individuals (Soroker *et al*., 1998). The hydrocarbon-transfer studies further demonstrated that there is a correlation between the mode of transfer and its magnitude. In species that perform trophallaxis, transfer within 24 h may reach 42% of the PPG content, e.g. in *Camponotus fellah* (Boulay *et al*., 2000b), while reaching only 3.2% in *P. apicalis*, which does not trophallax (Soroker *et al*., 1998). However, transfer in these studies was measured only in encounters between two individuals (called later 'dyadic' encounters), so conclusions regarding cue transfer in whole colonies are limited.

Rate of cue transfer is apparently a major factor, determining the speed at which the odours of emerging workers in the colony can be incorporated into the gestalt: i.e. how rapidly will they acquire the odours of other nestmates as well as contribute their own odour to the gestalt? The objectives of the present study were to demonstrate the occurrence of a gestalt colony odour by following the dynamics of the flow of radioactively labelled hydrocarbons in a group of 11 ants. This should provide a reasonable simulation of the flow of hydrocarbons in the entire colony. We compared these dynamics in two species with populous colonies, one that performs trophallaxis and one that does not. *Camponotus fellah* was chosen because an earlier study had demonstrated that this species has high trophallactic activity and a high rate of hydrocarbon transfer (Boulay *et al*., 1999); *Aphaenogaster senilis* Mayr (Myrmicinae) was chosen as a member of a genus that does not perform trophallaxis (Delage & Jaisson, 1969) but forms large colonies. In both species the existence of a gestalt colony odour was previously assessed, using individually isolated workers of *C. fellah* (Boulay *et al*., 2000a) and *A. senilis* (Lenoir *et al*., 2001).

It was predicted that the labelled hydrocarbons would be transferred to all the individuals of the group, so that all the participants would attain homogeneity and that homogeneity in the trophallactic *C. fellah* would be reached more rapidly than in the non-trophallactic *A. senilis*.

Using radioactive tracers we first measured hydrocarbon transfer in *A. senilis* in dyadic encounters and, by selectively using ants with blocked mouths, the prevailing mode of transfer was determined. The within-group rates of hydrocarbon transfer to confirm the gestalt formation systems were then measured, as well as the effect of transfer mode (trophallaxis or not) on the speed at which the gestalt was obtained. These experiments were accompanied by behavioural observations to determine the respective importance of trophallaxis and allogrooming in the time-budget of the ants.

Methods

Collection and maintenance of the ant colonies

Mature queenright colonies of *A. senilis* were collected in October 1999 in Doñana National Park, Andalusia (Huelva Province, south-west Spain). Colonies of *C. fellah* were established from mated queens collected during nuptial flight during March 1997–1999 in the area of Tel Aviv, Israel. Colonies were maintained in the laboratory in artificial nests under a controlled temperature of 24 ± 4 °C. The ants were fed three times a week with insects and provided with tap water and sugar water *ad libitum*. Colonies of *A. senilis* were also provided with a mixture of seeds.

The transfer of hydrocarbons between nestmates

To assess the rate of transfer between nestmates, donor ants were injected with 1 µCi [1–^{14}C] sodium acetate through the gaster intersegmental membrane, as described previously (Soroker *et al*., 1995). The mortality was very low. Only the ants that were in good condition and mobile after 24 h (25 ± 3 °C) were used for the transfer experiments. Each donor was presented with one recipient nestmate (dyadic transfer) or with 10 nestmates (group transfer). Dyadic encounters were conducted in Petri dishes (9-cm diameter) and group encounters were conducted in plastic boxes with a plaster floor. In encounters that lasted longer than 24 h the ants were fed and supplied with water. All dyadic encounters were stopped after 24 h by freezing the ants. Group transfer encounters were stopped after either 1, 3 or 6 days for *C. fellah* and *A. senilis*, with an additional 10-day period for the latter. In the highly polymorph *C. fellah* only median workers were used (weighing 10–12 mg non-fed). Workers of *A. senilis* are monomorphic and the weight of non-fed workers was 4–5 mg. In *C. fellah* the transfer rate was investigated between labelled media workers and 10 soldiers during a 24-h encounter. In the group transfer experiments the ants were observed daily for mortality. All dead ants (2% in both species) were removed immediately and were not included in the transfer calculations.

The occurrence of labelled lipids in the PPG and the thoracic cuticle was monitored for both donors and recipients. Dissected glands were immersed in 100 µL pentane, and cuticular lipids were extracted by immersing thorax and legs in 400 µL pentane for 5 min. The extracts were stored at – 20 °C until analysis when they were fractionated to classes of compounds by TLC using silica gel (Polygram Sil G, Machery

Nagel GmbH, Duren, Germany), and radioactivity of the hydrocarbon and non-hydrocarbon fractions was monitored by autoradiography (Fuji BAS 100 Phospho-Imaging analyser, Fuji PhotoFilm, Kanagawa, Japan), as described previously (Soroker *et al.*, 1995). Transfer of labelled material from donors to recipients was determined for each member of a pair or a group and for each tissue (PPG and cuticle) separately, and calculated as the percentage label found in each recipient out of the total label found in the donor(s) and recipient(s) combined. The total lipids (pentane-extractable) comprised approximately 65–75% hydrocarbons.

The relative roles of trophallaxis, allogrooming and other physical contact on the transfer of newly synthesized hydrocarbons in dyadic encounters were examined in *A. senilis* only. Either the donors or recipients, or both, had their mouths blocked with beeswax (see Soroker *et al.*, 1995). Encounters included all possible combinations of non-labelled, pre-labelled, blocked or non-blocked ants. Transfer in dyadic encounter in *C. fellah* had been investigated earlier (Boulay *et al.*, 2000b) and assessment of the role of trophallaxis on the transfer using mouth-blocking experiments was made previously on *Cataglyphis niger*, a formicine ant exhibiting similar trophallactic activity to *C. fellah* (Soroker *et al.*, 1995).

Behavioural observations

In the dyadic encounters of *A. senilis* the behaviours of both ants were recorded simultaneously every 10 min during the first 6 h. Behavioural items were classified into five categories: trophallaxis, selfgrooming, allogrooming, other physical contact (antennal and body contacts) and non-contact. Data are expressed as percentages of time devoted to any behaviour. In-nest behavioural measurements of self- and allogrooming were conducted on five workers from two different colonies for 15 min of each hour, from 09.30 to 20.30 hours, for a total of 3 h, using a Psion event recorder (Psion, Oxford, U.K.). We observed only in-nest workers, assuming that they are at the centre of the gestalt exchanges.

Statistics

Data are presented as mean ± SEM. We used the non-parametric Kruskal–Wallis test for global comparisons. When global analysis gave a significant effect, intergroup comparisons were then tested with the non-parametric Mann–Whitney U-test corrected for the α level of probability. To compare the distributions of frequencies of transfers we used the Kolmogorov–Smirnov test. A significance level of $P = 0.20$ was chosen because we predicted that the distributions would not differ from a normal distribution (second order error). All statistics were made with Statistica software.

Results

Dyadic encounters

Selective blocking of the mouth of worker *A. senilis* had a significant effect on the transfer of hydrocarbons into the PPG
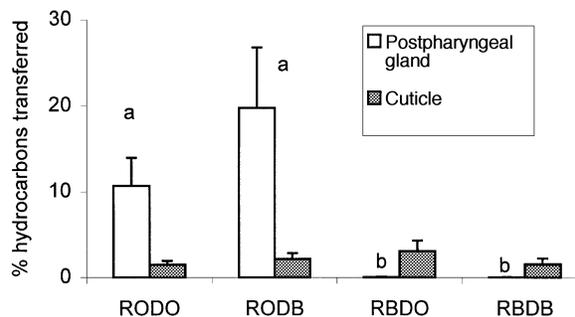
Fig. 1. Transfer of radioactive hydrocarbons in *Aphaenogaster senilis* to the postpharyngeal gland and the cuticle of recipient in dyadic encounters (mean ± SEM). Different letters indicate significant differences for postpharyngeal gland. n = number of dyads. RODO: Recipient Open/Donor Open ($n = 14$), RODB: Recipient Open/Donor Blocked ($n = 6$), RBDO: Recipient Blocked/Donor Open ($n = 12$): RBDB: Recipient Blocked/Donor Blocked ($n = 7$).

of the recipients in the dyadic encounters (Fig. 1, $P < 0.0001$, $n = 6$). Hydrocarbon transfer to the PPG in control groups reached 10% ($n = 14$), compared with 20% transfer when recipients with open mouth encountered blocked donors. However, this was not significantly different regardless of whether the donor's mouth was blocked or not ($P = 0.19$). Transfer to the PPG was abolished when the recipient too had a blocked mouth ($n = 7$ and $n = 12$, respectively). The levels of transfer to the cuticle were always lower (between 2 and 5%) than those to the PPG, and were not affected by blocking of the mouth ($P = 0.59$).

Group tests

After injection, the total amount of radioactivity in the pentane-extractable lipids in the PPG or the cuticle (donors and recipients included) did not change beyond the first 24 h and for up to 10 days. Exceptionally low biosynthetic rates were observed in the 3-day experiments with *C. fellah*. This, however, did not affect the results because transfer values were always calculated relative to the total biosynthesis in the specific experiments.

Figure 2(a) depicts the mean percentage of hydrocarbon transfer into the PPG and cuticle for *C. fellah* recipient workers. Although variability in transfer was large, there was a significant elevation in transfer when the duration of encounter increased ($P < 0.0001$ for PPG and cuticle). Transfer to the PPG after 1 and 3 days did not differ significantly and amounted to 4–5% ($P = 0.046$ NS, threshold being 0.017), but increased significantly to 7% after 6 days (1 day vs. 6 days $P = 0.0002$; 3 days vs. 6 days $P < 0.001$). Transfer to the cuticle increased significantly between 1 and 3 days (0.8 and 1.4%, respectively, $P = 0.001$) but remained unchanged thereafter (3 days vs. 6 days, $P = 0.43$). The donor transferred progressively more of the labelled hydrocarbons (Fig. 2b; $P = 0.004$); between 50 and 55% during the 1–3-day period,
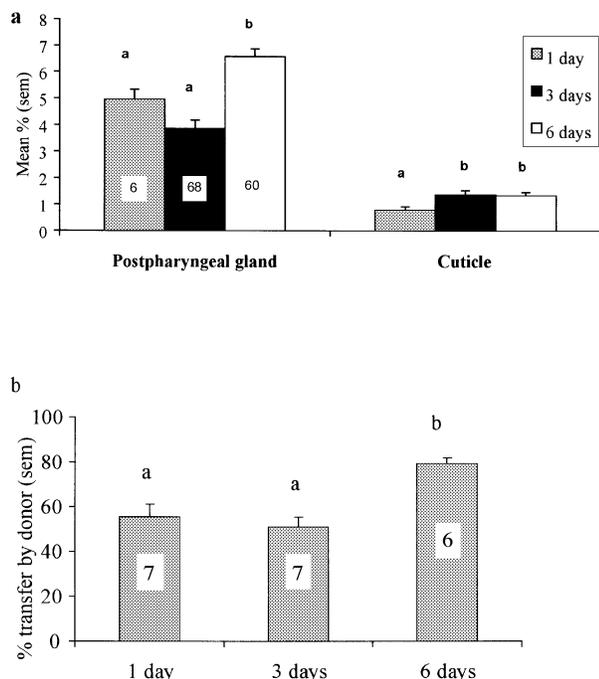
Fig. 2. Transfer of radioactive hydrocarbons in *Camponotus fellah*. (a) Percentage transferred to each recipient in the postpharyngeal gland or cuticle. (b) Total percentage transfer by each donor. Different letters indicate significant differences. Numbers within the columns indicate the sample sizes.

Fig. 3. Transfer of radioactive hydrocarbons in *Aphaenogaster senilis*. (a) Percentage transferred to each recipient in the postpharyngeal gland or cuticle. (b) Total percentage transfer by each donor. Different letters indicate significant differences. Numbers within the columns indicate the sample sizes.

and 75% after 6 days of encounter. Assuming an even distribution to all ants (one donor + 10 recipients), each participant was expected to possess, in the PPG and cuticle combined, 9.1% of total radioactivity. In fact, however, the donor retained significantly more radioactive hydrocarbons than expected (25% vs. the expected 9.1%). The amount of radioactivity on the cuticle presented in Fig. 2 represents extracts of thorax and legs only, rather than the whole cuticular surface. We therefore extrapolated the transfer to the whole cuticular surface, using the formulae: S = wet mass 0.67 * 12 (Edney, 1977; Johnson, 2000), and assuming that the repartition of hydrocarbons is homogeneous on the body, as indicated by Bagnères & Morgan (1990). After correcting for the donor's lesser contribution and the worker's body surface, the amount of transfer both to the cuticle and the PPG of the recipients after 6 days was not different from the expected (6.97% corrected observed data vs. 7.50% expected for total radioactivity).

In the encounters between a prelabelled median worker and soldiers, total transfer from the donor was 67.5 ± 7.3% (for 24 h encounter). Each individual soldier received 6.10 ± 0.6% to the PPG and 0.65 ± 0.1% to the cuticle.

Figure 3 depicts comparable data for transfer in *A. senilis* over a 10-day period, revealing a significant increase with time ($P < 0.0001$, Fig. 3a). The transfer into the PPG of the recipients increased progressively, reaching 6% at 10 days.

Increase in the cuticle followed a similar progression, but the difference between 6 and 10 days was not significant (6 vs. 10 days, $P = 0.70$). Accordingly, the amount given by the donor increased regularly, with only 28% being transferred after 1 day, and 73% after 10 days ($P = 0.0005$). In *A. senilis*, as some workers died in the 10-day experiment, the theoretical mean for an equal sharing should have been 8.1%, which corresponds to the 8.02% observed data (and 7.50% for the corrected data as indicated above).

Figure 4 presents the distribution of transfer amounts in *C. fellah* for 1, 3 and 6 days, and the corresponding calculated curves. The data distribution for the PPG after 1 day (Fig. 4a), was non-significantly different from a normal distribution (Kolmogorov–Smirnov test, $P > 0.20$). This was true also for the longer periods of encounters (3 days, $P > 0.20$; 6 days, $P > 0.20$). For the cuticle (Fig. 4b), the homogenization process was slower, with the 1 and 3 day curves being significantly different from normality ($P < 0.01$ and $P = 0.15$, respectively), but being normal after 6 days (6 days, $P > 0.20$).

The distribution of transfer amounts and the corresponding calculated curves for *A. senilis* are presented in Fig. 5(a,b). In this species, the process of mixing was considerably slower than in *C. fellah*. After 3 and 6 days the curves were significantly different from normal both for the PPG and the cuticle ($P < 0.05$ and $P < 0.10$, respectively). After 10 days the distribution was not significantly different from normal distribution in the PPG ($P > 0.20$) but not for the cuticle ($P < 0.20$).

Initial skewness of the distributions to the left were due to the numerous low transfer values, with some ants receiving little or no radioactive hydrocarbons. The numbers of zero

a) Postpharyngeal gland
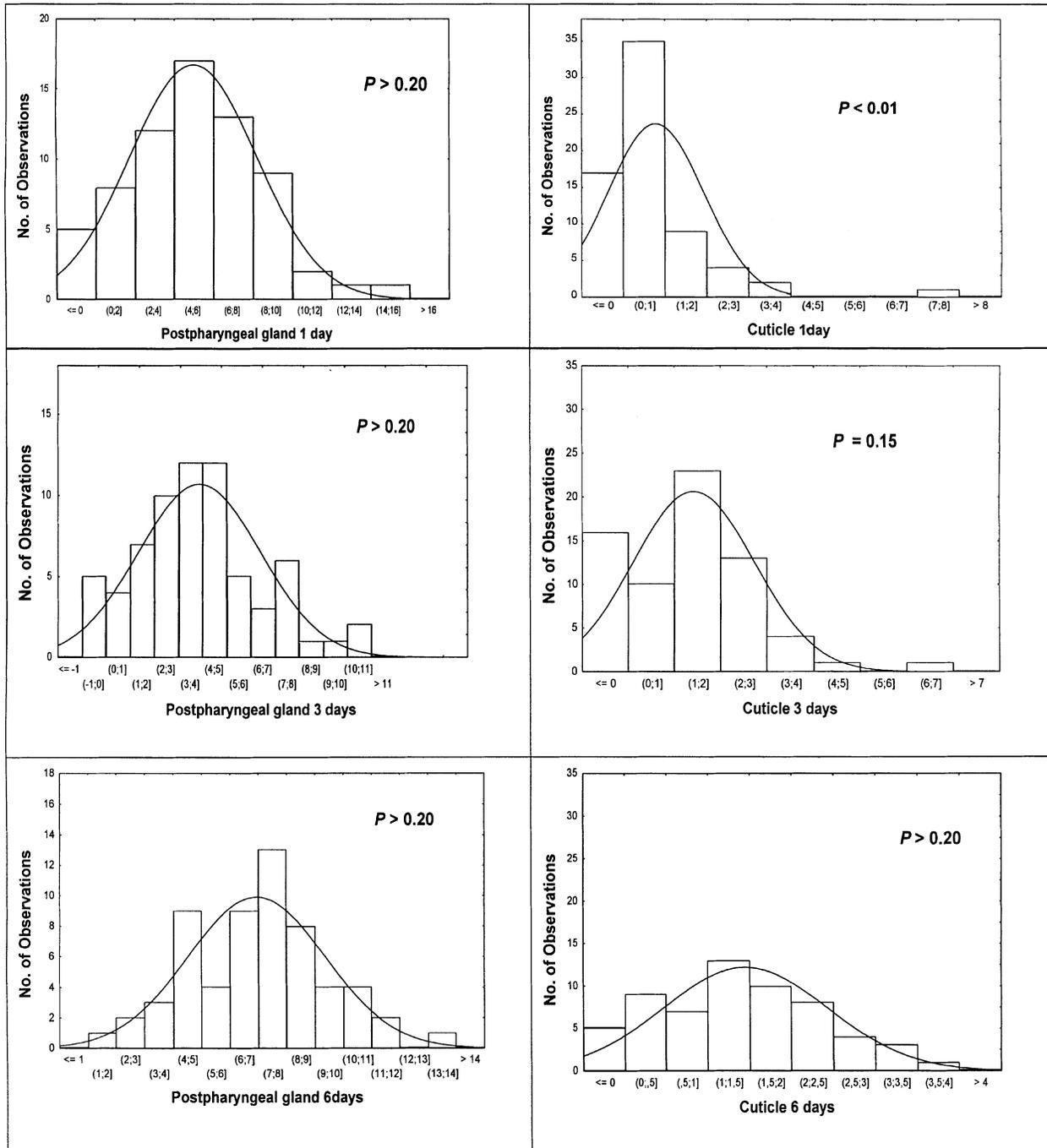
b) Cuticle

Fig. 4. Distribution of frequencies of transfer rates (%) in *Camponotus fellah* (observed data in histograms and normal distribution calculated in lines). (a) Postpharyngeal gland and (b) cuticle.

transfer values are given in Table 1. All the *C. fellah* workers possessed radioactive hydrocarbons in their PPG after 6 days, whereas it took 10 days for *A. senilis* workers. The spread on the cuticle was even slower. For both species, 10% of the ants were not labelled at all after 6 days, and for *A. senilis* 6% of the workers remained non-radioactive even after 10 days.

(a) Postpharyngeal gland **(b) Cuticle**
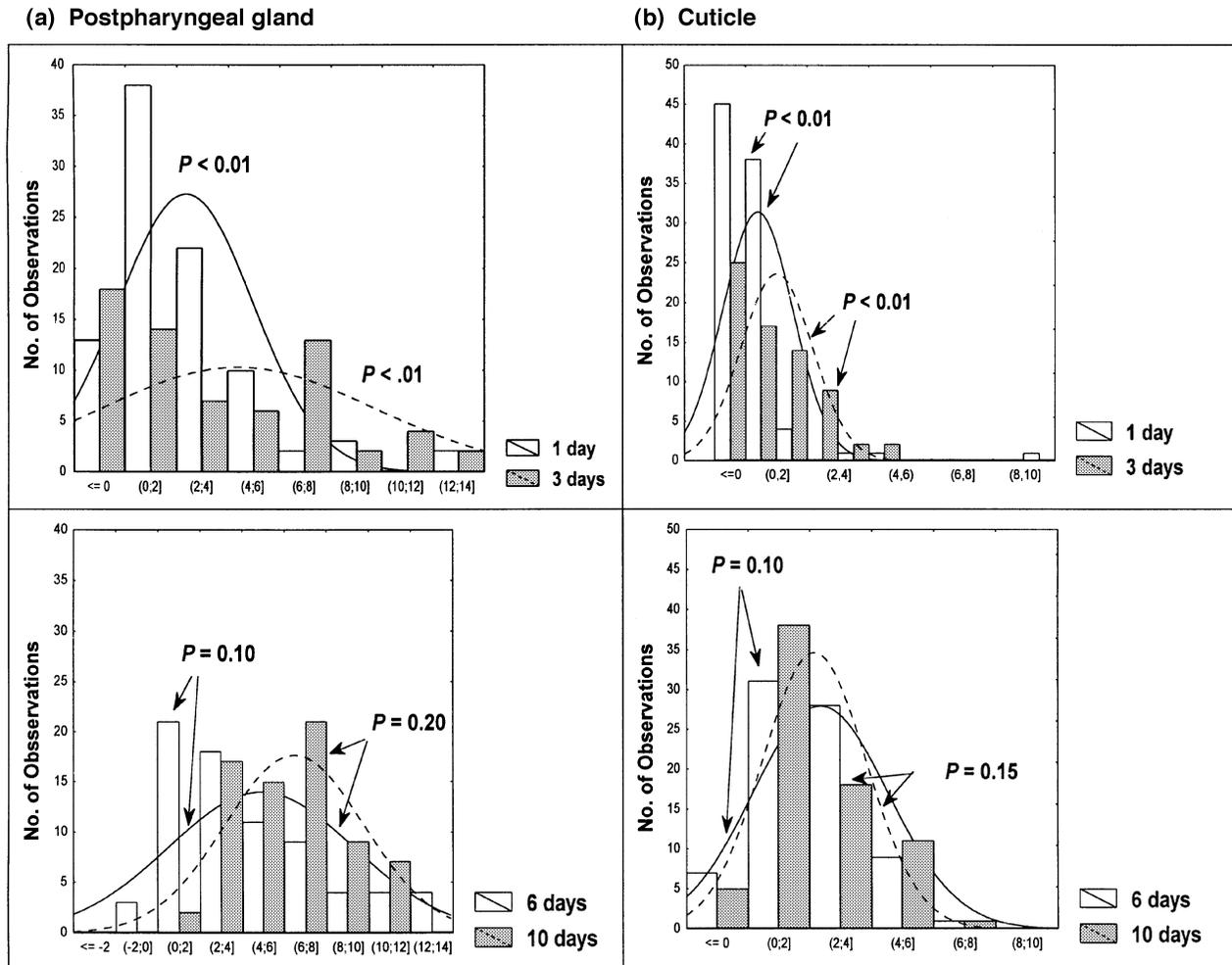
Fig. 5. Distribution of frequencies of transfer rates (%) in *Aphaenogaster senilis* (observed data in histograms and normal distribution calculated in lines). (a) Postpharyngeal gland and (b) cuticle.

The number of partners influenced the speed of distribution. In the dyadic tests the total transfer rate was low in the first 24 h (12% in *A. senilis* and 43% in *C. fellah*), whereas it reached 28 and 56%, respectively, in the group tests, probably due to the greater number of interactions.

Behaviour

We never observed any trophallaxis-like behaviour in *A. senilis*, either in dyadic encounters or inside the nest. By contrast, in *C. fellah* trophallactic activity occupied 4% of the ants' time. In dyadic encounters, both species performed allogrooming but at different levels: 1.1% for *C. fellah* and 7.2% for *A. senilis*. Selfgrooming and other physical contacts were very variable. Within-nest observations of unmanipulated colonies confirmed the frequencies of allogrooming in both species, indicating that it was not linked to experimental conditions.

Table 1. Percentages of recipient ants that did not receive any radioactive hydrocarbon, either in postpharyngeal gland (PPG) or in the cuticle (letters in columns indicate significantly different levels with test of difference between two proportions)

Days	*Aphaenogaster senilis*			*Camponotus fellah*		
	PPG	Cuticle	n	PPG	Cuticle	n
1	14.4[a]	50.0 [a]	90	16.0 [a]	55.6 [a]	68
3	26.1[a]	36.2 [a]	69	16.0 [a]	52.5 [a]	68
6	3.9[b]	9.1 [b]	77	0 [b]	11.8 [b]	60
10	0[b]	6.4 [b]	78	–	–	–

Discussion

Continuous flow of recognition cues takes place between colony members. Earlier studies as well as the present one

Table 2. Frequencies of behavioural items (mean ± SEM) observed in the recipient during the first 6 h of encounters between a prelabelled (donor) and a non-labelled (recipient) ant and rates of transfer to the postpharyngeal gland (PPG) and the cuticle to the recipient in 24-h encounter

| Subfamily | Species | Behavioural item | | | | Hydrocarbon transfer | | |
		Tro-phallaxis	Self-grooming	Allo-grooming	Other physical contact	To PPG	To cuticle	n
Formicinae	*Camponotus fellah*[1]	4.0 ± 0.9	4.8 ± 0.9	1.1 ± 0.4	76.4 ± 4.4	41.9 ± 5.21	1.3 ± 0.14	11
	Cataglyphis niger[2]	2.42 ± 0.6	11.1 ± 1.2	1.7 ± 0.5	25.4 ± 2.5	19.7 ± 3.29	1.2 ± 0.17	32
	Formica selysi[3]	0.14 ± 0.14	0.7 ± 0.2	0.7 ± 0.14	62.6 ± 6.8	13.6 ± 2.08	2.2 ± 1.36	10
Myrmicinae	*Manica rubida*[3]	0	3.4 ± 0.8	1.6 ± 0.6	36.9 ± 9.3	17 ± 4	5.7 ± 0.57	7
	Aphaenogaster senilis	0	4.8 ± 0.9	7.2 ± 3.5	31.9 ± 3.7	10.7 ± 7.05	1.5 ± 0.42	14
Ponerinae	*Pachycondyla apicalis*[4]	0	7.3 ± 1.1	0.5 ± 0.3	42.2 ± 2.8	3.2 ± 0.78	2.0 ± 0.74	15

[1]Boulay *et al.* (2000a).
[2]Soroker *et al.* (1995).
[3]Vienne *et al.* (1995).
[4]Soroker *et al.* (1998).

have demonstrated, using radioactive hydrocarbons as markers, that these exchanges can be accomplished either by trophallaxis, allogrooming or other physical contact. Opposing this tendency for gestalt creation is the time-dependent shift in cuticular hydrocarbon composition exhibited by individual ants (Boulay *et al.*, 2000a; Lenoir *et al.*, 2001; Lahav *et al.*, 2001), and the fact that newly emerging ants are constantly adding to the odour diversity in the colony. Therefore, assessment of rate of cue flow between nestmates is imperative for understanding the formation of the gestalt. We have attempted to address this question by measuring the rate of transfer between a single ant and 10 of her nestmates, a situation that we believe represents a better approximation of the process by which homogeneity is achieved in intact colonies.

In our study, the total radioactivity in hydrocarbons did not change significantly between 1 day and 10 days after injecting the radioactive acetate precursor, indicating that the bulk of radioactive hydrocarbons was produced within the first 24 h. This is probably because acetate is a very general precursor, and therefore the labelled pool was mostly exhausted within 24 h. However, as the donor still retained 25% of the radioactivity after 10 days (vs. 9.1% expected in the case of equal distribution) we cannot exclude the possibility that low levels of radioactive hydrocarbons were newly synthesized during this period. These may originate from existing radioactive acetate or from turnover of other radioactive substances. Nevertheless, we can assume that in all probability all the labelled hydrocarbons found in the recipients originated from the donor, and were the result of a sharing between participants.

Cue transfer between worker *A. senilis* has not previously been assessed together with behavioural observations (Lenoir *et al.*, 2001). We therefore first ascertained that trophallaxis is not present in this species and, using selectively mouth-blocked ants, assessed the effect of transfer modality on its magnitude. Mouth blocking of the donor in *A. senilis* did not

prevent hydrocarbons transfer to the PPG, provided that the recipient's mouth was not blocked. Because trophallaxis was impossible in this case, the accumulation of hydrocarbons into the PPG of the recipient must have been the consequence of allogrooming. The absence of trophallaxis on the one hand and the intensity of allogrooming on the other were further ascertained in the behavioural observations, both in the dyadic encounter and within the nest. The absence of trophallaxis in the genus *Aphaenogaster* was also indicated by experiments with coloured diets on *A. gibbosa* (Delage & Jaisson, 1969).

Our predictions on the dynamic of the gestalt were confirmed in both species: the sharing of hydrocarbons became more and more equitable, reaching the theoretical mean of 7.5–8% for each member of the group, with frequency distributions becoming progressively normal; and an equal sharing was obtained more rapidly in *C. fellah* (which exhibits trophallaxis) than in *A. senilis* (in which trophallaxis is absent). Rate of transfer also matched modality of transfer. *Camponotus fellah* donors had already passed on 55% of their labelled hydrocarbons after 1 day, and the frequency of distribution was normal for the PPG, indicating a high efficiency of transfer. Similar efficiency of trophallaxis in material transfer is observed in *Formica fusca*, where a single worker fed with radioactive iodine mixed with honey transfers the radioactivity to 75 nestmates within 140 h (Wilson, 1971). By contrast, it took *A. senilis* 10 days to reach 75% transfer.

Table 2 presents previously published behavioural data as well as percentages of hydrocarbon transfer into the PPG and the cuticle in various ant species. These are comparable because they were all obtained during dyadic encounters using the same methodology. According to the trophallactic behaviour, three types of species can be distinguished: species exhibiting an intense trophallactic activity, such as *Camponotus fellah* and *Cataglyphis niger*; species with a lower trophallactic activity, such as *Formica selysi* and *Manica rubida* (although in these species trophallaxis frequencies were low or absent under the experimental conditions during the

observation period, they are known to perform trophallaxis (Corbara & Errard, 1991); and species that do not practice trophallaxis at all, such as *P. apicalis* and *A. senilis*. From the limited species investigated, it can be suggested that for species practising trophallaxis the percentage of hydrocarbon transfer in dyadic tests is correlated with trophallaxis intensity. Linked with the group transfer data obtained in this study, this confirms that the greater rates of trophallaxis enable a faster update of the gestalt. Among the non-trophallactic species two patterns can be discerned with respect to gestalt formation: hydrocarbon transfer in *P. apicalis* was very low, amounting to only 3%, whereas in *A. senilis* it reached 11%, a value in the range calculated for trophallacting species. This high transfer can be attributed to allogrooming behaviour that was comparatively intense in *A. senilis*. Whereas in all other species this behaviour did not exceed 2%, it was 7.2% in *A. senilis*, which appears to compensate for the absence of trophallaxis in the transfer of gestalt cues, and to enable the establishment of a real gestalt in this species, although its dynamics were slower than in trophallacting ant species. In-nest behavioural observations demonstrated that this high level of allogrooming was not an artefact of the dyadic condition used in our experiments. Allogrooming in *P. apicalis* is rather low (0.5%) and the transfer between individuals can also be explained by other physical contact followed by selfgrooming (Soroker *et al.*, 1998). This raises the question of whether a gestalt is really achieved in *P. apicalis*, and the nature of the dynamics of hydrocarbon transfer in an entire colony. The low rate of active cue transfer seems to rule out the gestalt and suggests that colonial identity may simply be the association of individual odours, and that recognition may be based on the 'individualistic' model of Crozier (Crozier, 1987) rather than a real gestalt. This was previously noted in *Rhytidoponera confusa*, in which the gestalt component to the colony odour was estimated at 28%, whereas the individualistic component (72%) seemed to be more important (Crosland, 1989).

Ponerines like *P. apicalis* and *R. confusa* may have a colonial odour system that might be considered as close to a primitive state but is, nevertheless, likely to be sufficiently efficient in small monogynous colonies. The individualistic model of colonial odour may explain why intercolonial adoptions or formation of mixed colonies involving ponerine ants are so difficult (Errard & Jaisson, 1984; Jaisson, 1991). It is well known that callow workers are readily adopted by alien colonies, where they rapidly integrate the gestalt (chemical data in Nowbahari *et al.*, 1990), but in the ponerine ant *Ectatomma tuberculatum* alien workers are rejected after a delay of several weeks (Fénéron, 1993). These callows apparently produce only low quantities of hydrocarbons and thus, by being chemically insignificant, can be temporarily adopted by alien ants. However, as the ant matures it produces its own bouquet of hydrocarbons, and as transfer is very inefficient it is recognized as alien and thereby rejected from the nest. The same phenomenon may explain why alien cocoons are accepted in the archaic ant *Myrmecia*, but after emergence these alien callow workers are killed (Haskins & Haskins, 1950; Crosland, 1989; Jaisson & Taylor, in Jaisson, 1991).

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Corrigendum

Identification of feeding attractants in oak sap for adults of two nymphalid butterflies, *Kniska canace* and *Vanessa indica*, by Hisashi Ômura *et al*. **25**, 281–287 (2000).

We regret that concentrations of individual components given in Table 1 (p. 283) should be multiplied by 10 and those of ethanol, acetic acid and butane-2,3-diol shown on pp. 281 and 284 should thus read 9000, 5000 and 800 p.p.m., respectively.

We apologise for any inconvenience caused.