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Camponotus fellah colony integration: worker individuality necessitates frequent hydrocarbon exchanges

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Our aim was to test the existence of Gestalt colony odour in *Camponotus fellah*. We isolated individual workers to prevent trophallaxis, allogrooming and body contact. After 20 days, the cuticular hydrocarbon profile of the isolated ants diverged from that of the parent colony. Moreover, each isolated individual had its own specific blend. This procedure showed that after about 20 days of isolation there was a turnover of the colony odour, revealing the genetically expressed hydrocarbon profile of each individual. It also showed that the cuticular hydrocarbon profile is polymorphic, and that its homogeneity within a colony is maintained by frequent exchanges of hydrocarbons between workers. Behavioural observations of resident workers, in their nest, towards nestmates reintroduced after isolation indicated that a short isolation period (3–5 days), which induced a minor change in hydrocarbon profile, provoked frequent trophallactic solicitations. These were likely to permit the isolated ants to readjust their hydrocarbon profile to that of the ants in the mother colony. Longer isolation periods (20–40 days) induced a greater change in hydrocarbon profile and made the residents intolerant towards their introduced nestmates. Therefore, our results clearly support the existence of a Gestalt colony odour in *C. fellah*. They also show that since individual hydrocarbon production is dynamic, workers are obliged to exchange hydrocarbons continually (mainly by trophallaxis) in order to be in the Gestalt, and properly integrate into the colony.

Workers of eusocial insects behave in a manner that maintains colony integrity, that is, they tend to prevent parasitism and robbery by non-nestmates. Thus, eusociality based on 'nestmateship' requires a high degree of nestmate recognition (Lenoir et al. 1999). Since Fielde (1901, 1903) first emphasized the role of cuticular chemicals as recognition cues in ants, many correlative studies have suggested that cuticular hydrocarbons (CH) constitute these signals (reviewed in Vander Meer & Morel 1998; Lenoir et al. 1999). Recently, Lahav et al. (1999) presented direct evidence indicating that only the hydrocarbon fraction of the cuticular lipids allows nestmate recognition in *Cataglyphis niger*.

In species living in populous colonies it is unlikely that each member is recognized by its individual odour. Crozier (1987), enlarging the Crozier & Dix (1979) model, postulated that all the individuals within a colony share their own recognition cues to form a 'Gestalt colony odour'. The occurrence of a Gestalt colony odour in ants belonging to different subfamilies has been implied from both behavioural (Carlin & Hölldobler 1986, 1987; Stuart 1988; Crosland 1989; Tsuji 1990; Dahbi & Lenoir 1998) and chemical studies (Soroker et al. 1994, 1998; Meskali et al. 1995; Vienne et al. 1995). In *C. niger* individually produced hydrocarbons accumulate in the postpharyngeal gland, which opens into the mouth. Thus, hydrocarbons are exchanged mainly by trophallaxis and allogrooming (Soroker et al. 1995a, b).

Despite its uniformity, colony odour is dynamic, that is, the relative proportions of the different CH classes change over time (Vander Meer et al. 1989; Provost et al. 1993; Nielsen et al. 1999). According to the Gestalt hypothesis, two opposing processes may affect colony odour. On the one hand, CH profiles of individuals would change over time and result in odour diversification among colony members. On the other, continuous exchange between nestmates would lead to odour homogenization within the colony. The end result would be a dynamic yet uniform colony odour. An alternative hypothesis postulates that the conservation of the uniformity of the colony odour is maintained by a parallel

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shift in all nestmates, thus conserving similarities between the individual CH profiles. These two hypotheses generate different predictions regarding nestmate recognition behaviour. The first hypothesis predicts that isolated workers would be outside the centre of the Gestalt and would not be reaccepted into their mother colony. The second hypothesis predicts that separating workers from the influence of the colony odour would have no effect on the acceptance rates of the workers when reintroduced into the colony.

Few studies have addressed this question and all used split colonies where the separated ants were still kept as groups (Provost 1989; Crosland 1990; Dahbi & Lenoir 1998). While this experimental design enables the assessment of colony odour dynamics, it does not allow one to distinguish between these two hypotheses. Although in most species workers die after prolonged social isolation, it is possible to keep *C. fellah* workers alive in complete social isolation for a few weeks (Boulay et al. 1999). Taking advantage of this, we attempted to distinguish between the two hypotheses. We first characterized the cuticular hydrocarbons in queenright workers and then assessed changes in CHs in individually isolated workers deprived of any colony influence. We then investigated whether the putative isolation-induced CH divergence influences nestmate tolerance. Finally, we analysed the influence of social isolation (and thus of queenlessness) on ovarian development to check whether the aggression shown towards the isolated workers results from a reproductive conflict between workers or from their discrimination as alien.

METHODS

We conducted experiments with workers from the media caste engaged in intranest tasks (showing little gaster distension) from queenright *C. fellah* colonies maintained in the laboratory for 1 year and composed of 200–400 workers each. These colonies were established in the laboratory by newly mated queens that were collected in Ramat Aviv, Israel, in February 1997. Colonies were reared at 30 ± 2°C in artificial nests made of plaster to maintain a constant humidity (Boulay et al. 1999). Each nest was connected to a foraging area ($30 \times 40 \times 20$ cm) where honey supplemented with amino acids and vitamins (Be Happy, Koppert, Basse Goulaine, France) and *Tenebrio* larvae were supplied twice a week.

For each colony, all the workers used in the behavioural and chemical analyses were isolated on the same day (day 0), irrespective of the length of the isolation period. They were kept individually in test-tubes (18×0.18 cm) with water and food ad libitum until the day of the experiment (from day 1 to day 40). This procedure had no apparent adverse effect, most mortality appearing after 60 days of isolation (R. Boulay, unpublished data).

Chemical Analysis

For this analysis we used ants from two colonies (24 and 25 workers, respectively). After a first stage of sedation at 4°C, the ants were killed by freezing (-20°C) and washed in 1 ml of pentane for 10 min. The solution was stored at -20°C until analysis. The samples were evaporated to dryness and redissolved in 50 µl of pentane containing pentadecane (212 ng) as internal standard, of which 1 µl was then injected into the gas chromatograph.

We first determined the identity of CH by gas chromatography coupled to mass spectrometry (VGM250Q) with a DB-5 fused silica capillary column (temperature programme: 60–270°C at 5°C/min; hold at 270°C for 30 min and then heated to 295°C at 20°C/min). The eluting hydrocarbons were identified by their fragmentation pattern. We compared CH profiles of isolated workers at days 3, 20 and 40 and of nonisolated workers at days 0 and 40 by GC equipped with a capillary column (temperature programmed from 100 to 280°C at 3°C/min).

Behaviour and Ovarian Development

We established seven sets of 10 isolated workers (two workers per colony, five colonies) corresponding to the following isolation periods: 0 (control) 1, 3, 5, 10, 20 or 40 days. At the end of the respective social isolation period (days 1–40), the test-tubes containing the isolated ants were connected individually to their respective mother colony's nest entrance. Thereafter, we recorded every 10 s for 5 min the reaction of resident ants in the nest towards the introduced workers. This was repeated five times, at intervals of 25 min to a total of 150 min of observations. Recorded behaviours were (1) antennal contacts, (2) allogrooming, (3) trophallaxis, (4) threats (opening the mandibles with gaster flexion) and (5) bites. We limited experiments to 40 days of isolation to have a minimum observable aggression effect, longer isolation possibly leading to full rejection. Control groups were ants that were kept individually in test-tubes for only 20 min (the time necessary for them to become calm and stop running) before being reintroduced to their mother nest.

To verify ovarian development, we killed 40 ants (20 20-day isolated and 20 nonisolated workers from the same colony) as for the chemical analysis and dissected them. We did not check the ovarian development after 40 days of isolation since maturation is less than 15 days in other species such as *Cataglyphis cursor* (Cagniant 1984). Ovarian development was assessed by the presence of vitellogenic oocytes in the ovarioles.

Statistics

The total amounts of CH as well as the respective quantities of each CH class were compared by two-way ANOVA for two factors (colony identity and isolation period), followed by an LSD post hoc test when the differences were significant. The relative amounts of the major cuticular CHs were also compared with two-way MANOVA for two factors (colony identity and isolation period) and a discriminant analysis. For each colony, we compared the mean intragroup Euclidean distances by one-way ANOVA followed by an LSD post hoc test to

Table 1. The identity and relative amounts of cuticular hydrocarbons extracted from *Camponotus fellah* workers

Products (arranged by retention time)	Relative amounts
C_{17}	Trace
C_{18}	Trace
C_{19}	Trace
C_{20}	Trace
C_{21}†	**
C_{23}	Trace
C_{25}	*
7Me-C_{25}	Trace
C_{26}†	**
3Me-C_{26}	Trace
C_{27}†	****
11+13Me-C_{27}†	*
7Me-C_{27}†	***
3Me-C_{27}†	****
C_{28}†	**
8Me-C_{28}	*
4Me-C_{28}	Trace
$C_{29:2}$†	*
C_{29}†	**
15+13+11Me-C_{29}†	**
7,15DiMe-C_{29}†	***
3Me-C_{29}	*
C_{31}	*
15+13+11Me-C_{31}†	**
7,15,19TriMe-C_{31}†	***

Relative amounts are classified as: trace <1%; *<2%; **<5%; ***<10%; ****>10%.
†Peaks used in the statistical analyses.

compare the homogeneity of the hydrocarbon profile between workers of each group.

Since the behavioural variables did not follow a normal distribution (tested with the Shapiro–Wilks W test), we used the nonparametric two-tailed Kruskal–Wallis test for global comparisons. Intergroup comparisons were then tested with the nonparametric two-tailed Mann–Whitney U test. We applied a correction of the α threshold of acceptance that depended on the total number of possible paired comparisons. With seven groups (corresponding to seven isolation periods) there are 21 possible paired comparisons, so our new threshold was 0.05/21=0.002.

RESULTS

Chemical Analysis

Cuticular washes revealed the presence of 30 identifiable CHs (Table 1). The CH profile was composed of 12 alkanes (C_{17}–C_{31}), 15 monomethylalkanes, one dimethylalkane, one trimethylalkane and one alkadiene. However, some of the components could not be separated under our running conditions, revealing only 25 peaks in the chromatogram. Of these, 13 major peaks were taken into account for the statistical analyses (Table 1).

The total quantity of CHs was not significantly different between colonies nor between 3-, 20- and 40-day isolated ants or nonisolated ants sampled at days 0 and 40 (colony: $F_{1,39}$=0.29, P=0.59; isolation period: $F_{4,39}$=1.62, P=0.18; Table 2). Similarly, the isolation period had no significant influence on the quantities of alkanes and methylalkanes (alkanes: $F_{4,39}$=0.78, P=0.54; methylalkanes: $F_{4,39}$=1.66, P=0.19; Table 2).

A multiple analysis of variance on the assemblage of CHs (considering the relative intensity of the 13 selected peaks) from the two colonies and their respective isolated ants revealed a significant effect of the colony of origin and of isolation period (MANOVA: colony: $\lambda_{12,28}$=0.05, P<0.002; isolation period: $\lambda_{48,109}$=0.046, P<0.002). However, there was no significant interaction between these two factors (MANOVA: $\lambda_{48,109}$=1.39, P=0.08). To estimate the CH profile divergence as a function of isolation, we performed a discriminant analysis (DA) for each of the two experimental colonies. In colony 1 (Fig. 1a), the CH profile of the nonisolated ants at day 0 was significantly different from that of their isolated nestmates (DA: 3 days: $F_{8,12}$=3.46, P=0.026; 20 days: $F_{8,12}$=17.02, P<0.002; 40 days: $F_{8,12}$=7.38, P<0.002), but not from that of nonisolated day-40 ants (DA: $F_{8,12}$=1.53, P=0.24). In contrast, the difference between 40-day isolated and nonisolated nestmates sampled at day 40 was highly significant (DA: $F_{8,12}$=11.23, P<0.002). For colony 2, the hydrocarbon profile of nonisolated workers at day 0 was different from

Table 2. Quantities of cuticular hydrocarbons (total and by class) present in cuticular washes of *C. fellah* workers

	Nonisolated workers		Isolated workers			
Hydrocarbon class	Day 0	Day 40	Day 3	Day 20	Day 40	P
Colony 1						
Linear alkanes	1700±720	1500±360	2100±855	2000±225	2400±1035	0.44
Branched alkanes	4550±1530	5200±1395	5350±900	6800±2475	3700±1260	0.10
Total	6250±2430	6700±1800	7450±1295	8800±1035	6100±3195	0.07
Colony 2						
Linear alkanes	1800±810	2300±1080	950±385	2000±1440	3050±1125	0.61
Branched alkanes	7100±1935	4550±2655	6100±1755	4400±1755	4750±2205	0.30
Total	8900±2060	6850±2915	7050±2015	6400±2150	7800±2690	0.73

Nonisolated ants were sampled at day 0 (onset of the experiment) and at day 40 (end of the experiment). Isolated ants were analysed after 3, 20 and 40 days. Values are expressed in ng/ant, ($\bar{X}$±SD) and were compared with a two-way ANOVA followed by LSD post hoc test (P values).

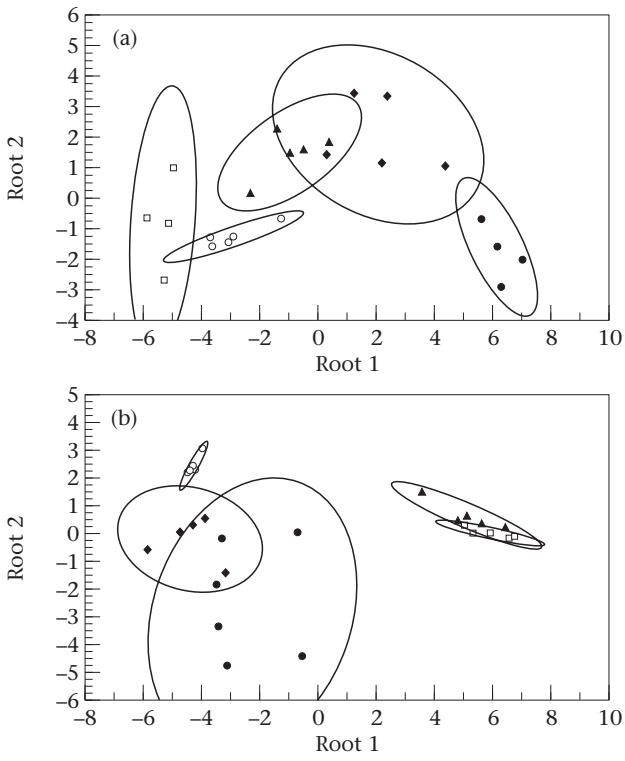

Figure 1. First two roots of the discriminant analysis conducted using the relative amounts of 13 major hydrocarbon peaks extracted from workers belonging to (a) colony 1 and (b) colony 2. Ellipses are 95% confidence intervals. □: Nonisolated workers on day 0; ○: nonisolated workers on day 40; ▲: workers isolated for 3 days; ◆: workers isolated for 20 days; ●: workers isolated for 40 days.

that at day 40 (DA: $F_{9,12}$=18.88, P<0.002; Fig. 1b). In this colony, 3 days of social separation were not sufficient to generate a significant divergence in the CH profile (DA: $F_{9,12}$=1.04, P=0.45), but longer social separations (20 and 40 days) led to a significantly different CH profile from that of nonisolated ants sampled at days 0 or 40.

For the two colonies, social isolation had a significant effect on the homogeneity of the CH profile as reflected by the larger ellipses (i.e. 95% confidence interval) of 20- and 40-day isolated workers in Fig. 1. The mean distance between the 40-day isolated workers was significantly higher than the mean distance that separated nonisolated workers, whether sampled at day 0 or day 40 (ANOVA: colony 1: $F_{4,41}$=5.74, P<0.002; colony 2: $F_{4,45}$=5.74, P<0.002; Table 3).

Behaviour and Ovarian Development

In general, upon reintroduction to their colony, the isolated ants immediately came into contact with the resident ants. This included amicable interactions such as antennal contacts, allogrooming and trophallaxis, but also aggressive interactions such as threatening behaviour and biting. In fact, the isolated ant could be attacked by one ant and solicited for trophallaxis by another at the same time.

Resident ants had frequent antennal contacts and allogrooming with reintroduced ants but there were no significant differences between isolated and nonisolated ants (Kruskal–Wallis: isolated: H_6=5.03, P=0.540; nonisolated: H_6=12.43, P=0.053; Table 4). However, social isolation had a significant effect on the frequency of trophallaxis (Kruskal–Wallis: H_6=27.18, P<0.002; Fig. 2a). The resident ants engaged in little trophallaxis with nonisolated ants when reintroduced into the nest (day 0, control). In contrast, trophallaxis with 1- and 3-day isolated nestmates was significantly more frequent (Mann–Whitney U test: 1 day: U=8, N_1=N_2=10, P<0.002; 3 days: U=4, N_1=N_2=10, P<0.002). The frequency of trophallaxis between 5-day isolated ants and the resident ants was intermediate, and not significantly different from nonisolated ants or from 1- or 3-day isolated ants.

Social isolation also had an important effect on the aggression of the resident ants towards the introduced nestmates (Kruskal–Wallis test: threats: H=37.86, P<0.002; bites: H=36.82, P<0.002; Fig. 2b, c). The frequencies of both aggressive behaviours were not significantly different from 0 until 20 days of isolation. However, the frequency of threats and bites increased significantly towards ants isolated for 40 days (Mann–Whitney U test: threats: U=7, N_1=N_2=10, P<0.002; bites: U=2, N_1=N_2=10, P<0.002).

None of the 40 dissected ants had developed oocytes.

DISCUSSION

In ants, temporal changes in the relative CH composition have been shown in field colonies of *Solenopsis invicta* (Vander Meer et al. 1989) and of *Formica truncorum* (Nielsen et al. 1999) as well as in laboratory-maintained colonies of *Leptothorax lichtensteini* (Provost et al. 1993). This seems to be the case also in *C. fellah* (nonisolated workers). Since environmental conditions (such as food, temperature) were constant in our study this shift may result from a continual modification of the colony's

Table 3. Euclidean distances ($\bar{X}$±SD) that separated the hydrocarbon profiles of two workers from the same group

	Nonisolated		Isolated		
	Day 0	Day 40	Day 3	Day 20	Day 40
Colony 1	6.38±3.23^{ab}	2.98±1.61^{a}	8.44±2.97^{bc}	10.53±3.69^{c}	10.02±4.68^{c}
Colony 2	4.01±1.53^{a}	9.99±3.82^{b}	4.27±2.17^{a}	13.10±5.82^{bc}	14.15±5.63^{c}

Different letters indicate significant differences (one-way ANOVA with LSD post hoc test).

Table 4. Frequencies (number of interactions per 25 min) of antennal contacts and allogrooming of resident ants towards workers isolated for different durations and then reintroduced into their mother colony

	Isolation duration (days)						
	0	1	3	5	10	20	40
Antennal contacts	62	88	94	89	77	70	97
	74	103	113.5	101	92	85	101
	120	131	123	124	101	110	111
Allogrooming	67	29	51	26	39	3	25
	76.5	67	60	39	51	10	43
	91	90	72	47	76	74	53

Values are first, second and third quartiles. None of the values was significantly different (Kruskal–Wallis test, N=10 introduced workers).

composition (e.g. ratio of soldiers:workers, genetic drift due to multiple insemination). Social isolation was also followed by progressive changes in cuticular CHs. The fact that we could not detect differences in the amounts of CH (even for classes of hydrocarbons) seems to rule out the possibility that the isolation situation, which is unusual and probably stressing, perturbed CH biosynthesis. It is therefore more probable that the absence of CH exchanges with the rest of the colony led to a divergence in the profile. Interindividual hydrocarbon exchanges as the basis for creating a uniform colony odour have been shown with radiolabelled markers, in *Formica selysi/Manica rubida* mixed colonies (Vienne et al. 1995), *C. niger* (Soroker et al. 1994), *Pachycondyla apicalis* (Soroker et al. 1998) and *C. fellah* (Boulay et al. 2000) where hydrocarbon exchanges are very intensive (in a dyadic situation, one worker can exchange up to 42% of hydrocarbon in 24 h). A 20-day isolation period appears to be sufficient for clearing the pool of CH that results from exchange with other colony members, and thus enabling individual expression. Although all the ants were isolated under the same conditions, the interindividual differences in CH profile increased with the prolongation of the isolation period (as shown by the larger 95% confidence ellipses of isolated workers on Fig. 1). This shows that CH biosynthesis is polymorphic, and that in *C. fellah* the homogeneity of CH between nestmates results from a Gestalt phenomenon, that is, the blending of the individually produced CHs. Thus, the uniformity of the CH profiles, despite their change over time, results not from a parallel shift in all nestmates, but from a constant homogenization of the CHs produced by all colony members. Queen and/or environmental cues that may be involved in the formation of colony odour, as postulated in *Camponotus floridanus* (Carlin & Hölldobler 1987), will also diminish in influence over a period of 20 days. This is also evident from the behavioural data discussed below.

Social isolation also led to a change in behaviour of the resident ants towards their introduced isolated nestmates. Long periods of isolation (20–40 days), which led to the greatest divergence in CHs in the isolated ants, also made the resident nestmates intolerant. This isolation-induced aggression was not caused by a putative conflict between workers after the separation from the queen, as was proposed for *Aphaenogaster cockerelli*, *Rhytidoponera confusa* and *Harpegnathos saltator*. In these species, workers kept in queenless groups developed ovaries and were consequently attacked by their queenright nestmates as part of a worker policing system (Hölldobler & Carlin 1989; Crosland 1990; Liebig et al. 1999, respectively). In contrast, none of the isolated *C. fellah* developed ovaries even after the longest isolation period. A modification of the colony recognition cues is therefore probably at the origin of the intolerance. Intolerance towards isolated workers started after about 10–20 days, the time necessary for the CHs to change and assume an individual profile distinct from the colony profile. As in previous correlative studies (Lenoir et al. 1999), this provides another striking parallelism between the shift in CH profile and elevated aggression. Since CHs are postulated to be the main chemical underlying nestmate recognition in several ant species, the divergence from the colony Gestalt induced by isolation may have caused the rejection of the isolated workers. However, CHs involvement in nestmate recognition in *C. fellah* should be confirmed by direct behavioural tests as in *C. niger* (Lahav et al. 1999). Our results emphasize the importance for each worker in the colony to exchange hydrocarbons frequently with her nestmates in order to contribute to the Gestalt and so to be integrated into the colony. In *C. niger*, the cue transfer system required by a Gestalt system is mainly provided by trophallaxis (Soroker et al. 1995a, b). Recent observations in *Cataglyphis iberica* indicate that trophallaxis might allow a uniform odour to be re-established between workers reunited after 8 weeks of separation (Dahbi et al. 1999). In *C. fellah*, 1–5 days of complete social separation was enough to induce long trophallaxis events that were independent of motivation to feed (Boulay et al. 1999). These may have also permitted the isolated worker to readjust its CH profile to resemble that of her nonisolated nestmate.

Only a few resident workers expressed aggression towards isolated nestmates. Moreover, other workers behaved amicably. This suggests the existence of polyethism regarding nestmate recognition capacities. Our experimental design, observing the response of ants within the nest rather than in a dyadic encounter,

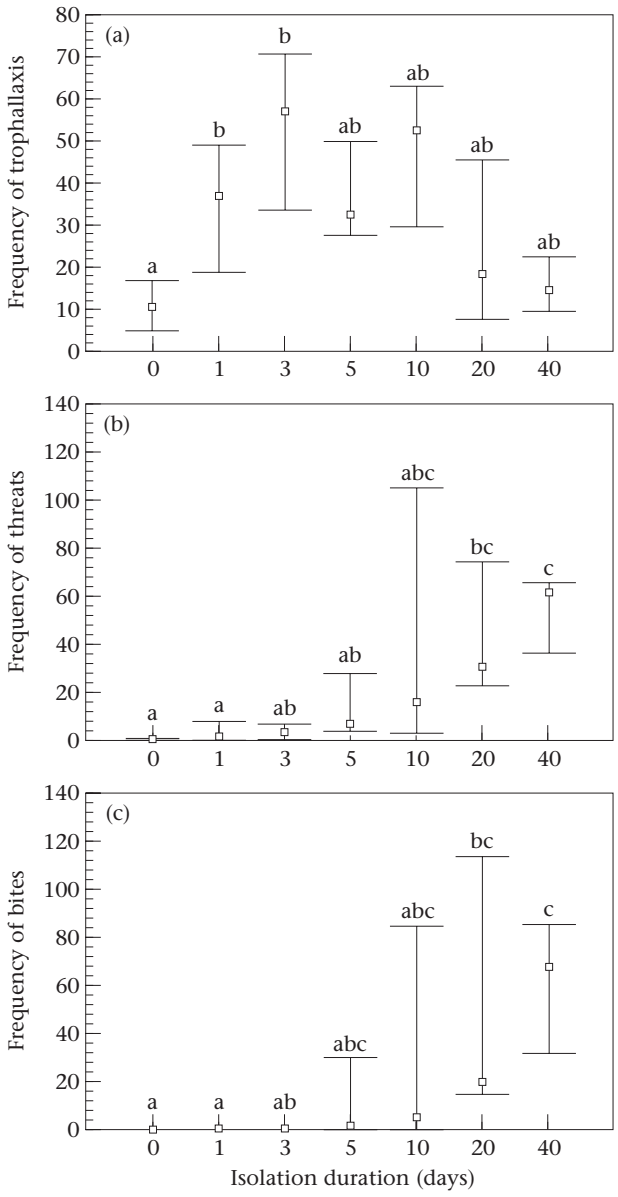

Figure 2. Frequencies (number of interactions per 25 min) of (a) trophallaxis, (b) threats and (c) bites (medians, first and third quartiles) between resident ants and their nestmates isolated for 0, 1, 3, 5, 10, 20, 40 days and reintroduced into their mother colony. For each worker, observations lasted 25 min, during the first 150 min after the introduction. Different letters indicate significant differences (Mann–Whitney *U* test: α=0.002, *N*=10).

allowed us to observe the response of the more sensitive individuals (guards?) even though they were not numerous. It also takes into account the influence of context on the discrimination threshold, as shown for *Acromyrmex subterraneus* (Viana & Lenoir 1994) and for the paper wasp *Polistes dominulus* (Starks et al. 1998). The higher rejection rates of ants after longer isolation periods support the differential threshold sensitivity of the resident workers. We suggest that the longer the isolation period, the more ants become sensitive to the odour changes and display aggressiveness. The higher aggression shown towards these workers counterbalances the trophallaxis attempts by the less sensitive resident individuals, resulting in the higher rejection rates.

Finally, our results support the existence of a Gestalt colony odour in *C. fellah*. We have shown that since individual CH production is dynamic and polymorphic, it is essential for nestmates to homogenize their CHs frequently to create a unique and uniform colony-specific profile. Lack of trophallaxis results in divergence from the colony odour, a fact that can be detected by nestmates with a low discrimination threshold resulting in the rejection of the divergent individuals. In field colonies of *C. fellah* this phenomenon is probably amplified since odour polymorphism should be larger than in our laboratory colonies, providing a strong selection force for the evolution of extensive trophallaxis.

Acknowledgments

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