

# Social isolation of mature workers affects nestmate recognition in the ant *Camponotus fellah*

R. Boulay \*, A. Lenoir

Institut de Recherche sur la Biologie de l'Insecte, UPRES A CNRS 6035, Faculté des Sciences et Techniques, Parc de Grandmont, Université François Rabelais, F-37200 Tours, France

Received 28 July 2000; received in revised form 12 November 2000; accepted 10 January 2001

## Abstract

This study investigates the role of social stimulation on nestmate recognition in mature workers of *Camponotus fellah*. We isolated 4-week-old workers before examining their behaviour in dyadic reunion tests. At the age of 4 weeks, workers are normally intolerant towards both allospecific and homospecific but allocolonial individuals. However, when they were isolated for up to 20 days, allocolonial aggressions decreased while allospecific aggression remained constant. Workers isolated for 20 days also engaged in allocolonial trophallaxis. These results suggest that workers need to be reinforced by social stimulation during their adult life to keep precise nestmate recognition capacities. We discuss our data under the perspective of recent neuroethological data in social insects to propose a mechanism for the formation of the neural template used in the nestmate recognition process. © 2001 Elsevier Science B.V. All rights reserved.

**Keywords:** Nestmate recognition; Social isolation; *Camponotus fellah*; Learning; Template formation

## 1. Introduction

It is generally accepted that eusociality means that individuals living in a colony unequally share reproductive tasks and that there is an overlap of at least two generations allowing offspring to help parents rear immature siblings. While the central question of eusociality excited sociobiologists over the last three decades (see recent arguments from Sherman et al., 1994 and Crespi and Yanega,

1995), one trait that characterises most eusocial insect species was quietly neglected: individuals have a particular tendency to search for and to keep social contacts with their nestmates and this has many consequences on colony life. For instance, worker–worker interactions are responsible for the plasticity in division of labour in regard to specific needs of the colony in the honeybee (Huang et al., 1998; Huang and Robinson, 1992, 1996) and in harvester ants (Gordon, 1989, 1996). Interactions between nestmates also mediate the colony activity cycle in *Leptothorax allardycei* (Cole, 1991a,b) and the ethogenesis in *Ectatomma tuberculatum* (Champalbert and Lachaud, 1990).

\* Corresponding author. Tel.: +33-972-36408766; fax: +33-972-36406991.

E-mail address: rapheal-boulay@hotmail.com (R. Boulay).

In ants, worker–worker interactions also influence colony defence. Most ant species are aggressive animals that attack any allospecific or allocolonial intruder. This general aggressiveness is partly controlled by behavioural and chemical cues originating from nestmates. For instance, in *Pheidole pallidula* behavioural stimulations from minor workers are responsible for the ontogeny of aggressive behaviours in soldiers (Aarab and Jaisson, 1992). The occurrence of releaser and maybe primer pheromones that elicit aggressive behaviours, are also reported in many species (see review from Van der Meer and Alonso, 1998).

Worker–worker interactions also affect the capacity to discriminate between nestmates and aliens. This mechanism consists of the comparison of the phenotype (olfactory signature) of any encountered individuals with a reference (template). Of course, nestmates' signatures must have similarities and the template must reflect these similarities. At least in some formicines and myrmicines, callows acquire both the signature and the template from their nestmates (see Lenoir et al., 1999). However, in the carpenter ant *Camponotus fellah* and several other species, the colony signature is not static, but changes over time, suggesting that the template does so as well (Van der Meer et al., 1989; Provost et al., 1993; Nielsen et al., 1999; Boulay et al., 2000a).

The aim of the present study was to determine whether social stimulation is necessary to maintain the capacity to reject aliens and to accept nestmates. Changing the social environment just after emergence from pupal stage increase tolerance of aliens when the individuals become mature. The originality of the present report is that it concerns mature individuals. Because old carpenter ants are aggressive, it is not possible to transfer them to another colony as was done in previous experiments with callows. However, old workers can survive for few weeks even if deprived of any contact with nestmates. Thus, rather than changing the social environment, we suppressed it for up to 20 days and then we conducted bioassays to measure the relative tolerance between nestmates and between allocolonial and allospecific aliens after isolation.

## 2. Materials and methods

### 2.1. Collection of ants and rearing conditions

Experiments were conducted with workers from five queenright colonies of *C. fellah* Dalla Torre and from two queenless colonies of *Camponotus vagus* Scop. Only minor workers that were involved in intra-nest tasks (mostly nurses) and that showed some degree of gaster distension were used. Preliminary observations during which workers were marked just 2 days after emergence indicated that they showed such gaster distension when at least 4 weeks old.

Colonies of *C. fellah* were established in the laboratory from newly mated queens that were collected at Ramat Aviv (Israel) 1 year before the experiment. Colonies of *C. vagus* were composed of approximately 300–400 individuals and some brood. They were collected at Rilly-sur-Vienne (France) and maintained in the lab for 2 months before the experiment. Colonies of both species were reared in artificial nests made of plaster to maintain a constant humidity (see Boulay et al., 1999 for more details). Temperature, humidity and light–dark cycle in the rearing room were  $25 \pm 2^\circ\text{C}$ ,  $60 \pm 5\%$  and 12:12 LD, respectively. Each nest was connected to a foraging area ( $30 \times 40 \times 20$  cm) where food (Bee Happy, Koppert, Biological system and *Tenebrio* larvae) was supplied ad libitum.

### 2.2. Experiment 1: social isolation effect on allocolonial aggression

Two hundred and sixty-six *C. fellah* minor workers were sampled in almost the same proportions from each of the five colonies, depending on availability. They were isolated in test tubes ( $18 \times 180$  mm) where they had ad libitum access to water and food (Bee Happy and *Tenebrio* larvae). They were kept in the tubes for 20 min (the minimum time for the ants to calm down), 5, 10 or 20 days. Bioassays consisted of dyadic reunions between individuals that were previously submitted to the same isolation duration, but that originated either from two different colonies (allocolonial encounters) or from the same colony

(homocolonial encounters, control). The tubes were connected one to each other to let the workers enter into contact by themselves without any manipulation that could generate stress. Behavioural items were recorded for 5 min from the first interaction.

### 2.3. Experiment 2: social isolation effect on allospecific aggression

Eighteen *C. fellah* workers and 18 *C. vagus* workers were sampled in almost the same proportions from the five colonies and two colonies, respectively. They were isolated in test tubes as previously described for 20 min or 20 days. Then, their behaviour was recorded while they were reunited in allospecific dyads for 5 min, as described in experiment 1.

### 2.4. Recorded behavioural items and statistics

We recorded the frequency and duration of all interactions using a Psion organiser. In order to assess the effect of the duration of isolation on the aggression expressed in homocolonial, allocolonial and allospecific encounters we used the aggression index (A.I.) elaborated by Hefetz et al. 1996:

$$\text{A.I.} = \frac{\sum_{i=1}^n \text{A.I.}i \times t_i}{T}$$

where  $T$  is the total time of interaction,  $\text{A.I.}i$  is a factor applied to each act regarding its degree of aggressiveness: non-aggressive interactions (antennal contacts, trophallaxis and allogrooming) were scored  $\text{A.I.}i = 0$ ; openings of the mandibles were scored  $\text{A.I.}i = 1$ ; flexions of the abdomen with or without visible spray of formic acid were scored  $\text{A.I.}i = 2$ ; bites were scored  $\text{A.I.}i = 3$ .  $t_i$  is the duration of each interaction. The index A.I. varies from 0 (no aggression) to 3 (all interactions are bites). We also recorded the total duration of trophallaxis.

In experiment 1 we compared aggression indexes in homocolonial versus allocolonial encounters and after 20 min, 5, 10 or 20 days of isolation with multiple analyses of variance for two factors:

‘type of encounter’ and ‘isolation duration’. Specific effects were determined by LSD post hoc tests. Total durations of trophallaxis were compared by the same statistics.

In experiment 2 we compared aggression indexes and the total duration of trophallaxis in allospecific encounters after 20 min (control) and 20 days of isolation by  $t$ -tests.

## 3. Results

### 3.1. Social isolation effect on allocolonial aggression

In the field, *C. fellah* is a monogynous species that builds very widespread nests. Although the border between neighbouring nests seems to overlap, the social closure is very high. In our laboratory tests, the aggression index A.I. was significantly higher in allocolonial than in homocolonial encounters (Fig. 1, two-tailed MANOVA:  $F_{1,133} = 64.0$ ,  $P < 0.001$ ). The factor ‘isolation duration’ also had a highly significant effect on A.I. (Fig. 1, two-tailed MANOVA:  $F_{3,133} = 4.0$ ,  $P = 0.008$ ). Moreover, there was a significant interaction between the factor ‘type of encounter’ (homo- vs. allocolonial) and the factor ‘isolation duration’ (Fig. 1, two-tailed MANOVA:  $F_{3,133} = 4.9$ ,  $P = 0.003$ ).

In homocolonial encounters, A.I. was low whatever the duration of isolation. On the contrary, A.I. in allocolonial encounters significantly decreased from  $0.56 \pm 0.10$  to  $0.10 \pm 0.03$  (LSD post hoc test,  $P < 0.001$ ). Most interactions between workers originating from different colonies and maintained for 20 min in the test tubes were threatening. However, after 20 days of social isolation A.I. between non-nestmates was as low as between nestmates (LSD post hoc test,  $P = 0.38$ ).

The total duration of trophallaxis also increased in allocolonial encounters. Both factors of ‘type of encounter’ and ‘isolation duration’ had a significant effect on the duration of trophallaxis (Table 1, two-tailed MANOVA,  $F_{1,133} = 19.6$ ,  $P < 0.001$ ; and two-tailed MANOVA,  $F_{3,133} = 18.3$ ,  $P < 0.001$ , respectively), but the interaction was not significant (two-tailed MANOVA:  $F_{3,133} = 1.4$ ,

$P = 0.10$ ). In fact, trophallaxis between nestmates increased from  $3.00 \pm 1.22$  s after 20 min of isolation to  $133.34 \pm 20.29$  s (that is approx. 45 % of the total duration of the test) after 20 days of isolation. The duration of trophallaxis between non-nestmates was also very short after 20 min of isolation ( $1.71 \pm 0.77$  s) and increased significantly after 20 days to  $55.50 \pm 9.21$  s. However, allocolonial trophallaxis remained significantly shorter than homocolonial ones.

### 3.2. Social isolation effect on the allospecific aggression

Encounters between workers of *C. fellah* and *C. vagus* were very aggressive. The aggression indexes were higher in allospecific encounters than between allocolonial encounters (Fig. 2). A.I. was not significantly affected by the duration of isolation ( $t$ -test:  $t_{18} = -0.35$ ,  $P = 0.72$ ). No inter-specific trophallaxis occurred between *C. fellah* and *C. vagus* whatever the duration of isolation.

## 4. Discussion

Our experiments showed that social isolation in mature workers leads to a specific decrease of allocolonial aggression. Two hypothetical expla-

nations were possible. First, the impossibility of contact with the colony could have decreased the general aggressiveness of the isolated individuals. Indeed, as indicated in the introduction, worker-worker interactions stimulate aggressiveness through pheromonal or behavioural communication. However, if social isolation would affect the general aggressiveness of the individual, we would expect an effect both in allocolonial and allospecific aggression. The results of the second experiment showed that allospecific encounters are as aggressive after 20 days than after 20 min of isolation. Thus, the hypothesis of a non-specific decrease of aggressiveness appears unlikely.

The second hypothesis is that social deprivation could specifically reduce the ability to recognise and discriminate between nestmates and aliens. The nestmate recognition process depends on the social environment. In many species, both the recognition labels and the template are acquired shortly after the emergence (Carlin and Hölldobler, 1986; Errard, 1986; Carlin et al., 1987; Errard et al., 1990; Stuart, 1992). In *C. vagus* and *C. pennsylvanicus* callows need to have contact with foragers and nurses of their colony to express normal nestmate recognition once they are mature (Morel, 1983; Morel and Blum, 1988). Results from Myrmicinae, Formicinae (including *C. fellah*) and Ponerinae indicate that workers

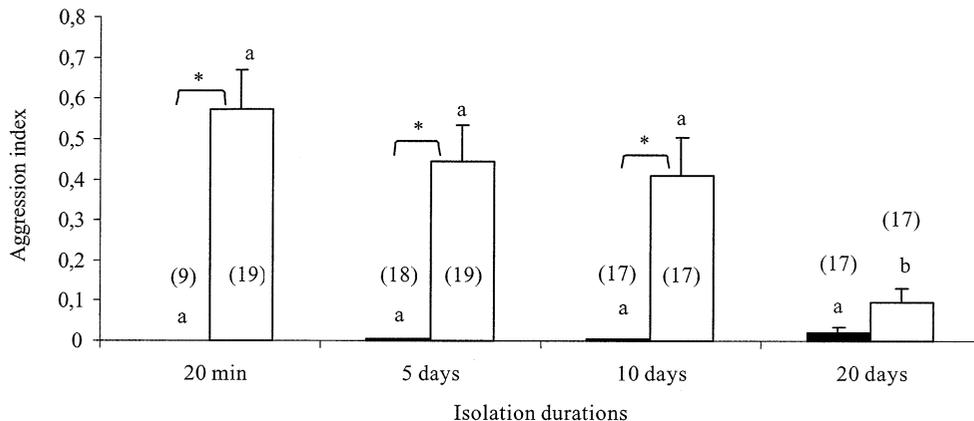


Fig. 1. Mean aggression index ( $\pm$  S.E.M.) regarding the isolation duration in homo- (black) versus allocolonial (white) encounters. Letters indicate differences between A.I. in homocolonial encounters over the duration of isolation. Letters indicate differences in A.I. in heterocolonial encounters. Stars indicate significant differences between A.I. in homocolonial encounters and A.I. in allocolonial encounters for the respective isolation duration. Numbers between parentheses are sample sizes.

Table 1

Total duration of trophallaxis in seconds (mean  $\pm$  S.E.M.) between *C. fellah* workers in homocolonial and allocolonial dyadic encounters<sup>a</sup>

	Isolation duration			
	20 min (control)	5 days	10 days	20 days
Homocolonial	3.00 $\pm$ 1.22 a	76.97 $\pm$ 7.09 b	50.70 $\pm$ 9.56 b	133.34 $\pm$ 20.29 c
Allocolonial	1.71 $\pm$ 0.77 a	12.95 $\pm$ 7.25 a	46.00 $\pm$ 17.8 b	55.50 $\pm$ 9.21 b
<i>P</i>	0.946	0.603	0.031	0.008

<sup>a</sup> Means followed by different letters indicate a significant difference between isolation period duration. *P* values indicate probability of significant differences between the duration of trophallaxis in both homocolonial and allocolonial isolation duration. (MANOVA followed by LSD post hoc test). Sample sizes are indicated in Fig. 1.

exchange cuticular hydrocarbons (Meskali et al., 1995; Soroker et al., 1995, 1998; Vienne et al., 1994; Boulay et al. 2000b), which are the only nestmate recognition cues so far identified in ants (Lahav et al., 1999). These exchanges of individually produced cues are responsible for the formation of a unique and homogenous colony odour. As the colony composition changes, its odour does as well and workers have to maintain social contacts in order to wear the same odour as their nestmates and to be integrated in the colony (Dahbi and Lenoir, 1998; Boulay et al., 2000a). This also suggests that workers may have to update their template continually throughout their adult life. The absence of stimulation by colony-specific cues for 20 days could have partially erased the workers' template, leading to confusion in nestmate recognition.

Fresneau and Errard (1994) and Lenoir et al. (1999) presented two hypothetical mechanisms to explain how the template could be updated regarding its nature. First, workers' template could be their own chemical signature. Then, nestmate recognition is a comparison between the signature of other individuals and its own signature. Under this hypothetical mechanism isolated workers would be more tolerant towards allocolonial conspecifics because their chemical signatures would become more homogenous. However, at least in *C. fellah* the exact opposite happens, that is social isolation induces a divergence of the individual cuticular hydrocarbon profiles (Boulay et al., 2000a). The second mechanism hypothesised by these authors is based on a neural template. The

olfactory characteristics of the colony are acquired shortly after emergence of a learning process (Jaisson, 1975). But, since the colony odour is not constant, the old memory must be erased or replaced by a new one, suggesting that colony characteristic learning is not limited to the precocious period but continues throughout the adult life. This system supports that workers would have to be frequently in contact with nestmates to maintain a precise neural template of the current colony odour. Our results are in agreement with this mechanism and suggest that the impossibility of maintaining contact with nestmates enlarges the neural template. After isolation, allocolonial signatures, which are slightly different, would no longer be discriminated from nestmates while

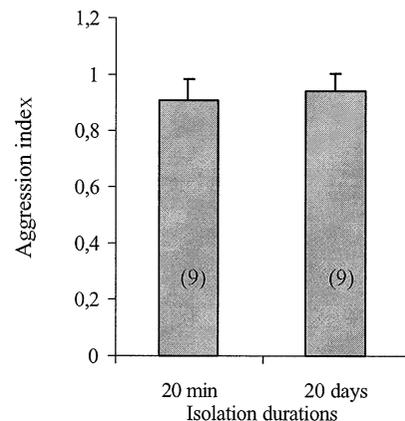


Fig. 2. Mean aggression index ( $\pm$  S.E.M.) regarding the isolation duration in allospecific encounters. There were no significant differences (*t*-test). Numbers between parentheses indicate sample sizes.

completely different allospecific signatures (*C. vagus* workers) would still be recognised.

It is noteworthy that social isolation provokes both a decrease of aggression and an increase of trophallaxis between allocolonial workers. Trophallaxis allows food and hydrocarbon transfers, but also has appeasing effects. Individuals that are aggressed sometime answer by offering trophallaxis to decrease the aggression (Bhatkar, 1979a,b; Heinze, 1996). In *C. fellah*, we have shown that need for trophallaxis increases after social isolation (Boulay et al., 1999, 2000a). Thus, it is possible that a reciprocal need for trophallaxis was in part responsible in reducing aggression after social isolation.

In a homocolonial context, isolation-induced trophallaxis can be inhibited by administration of octopamine. It strongly supports the idea that social isolation might induce a decrease in brain octopaminergic activity responsible for an increase of the need for trophallaxis (Boulay et al., 2000b). Though no physiological mechanism has yet been clearly proposed to explain how relevant cues are learned, octopamine agonists also improve nestmate recognition in young honeybee workers (Robinson et al., 1999). As octopamine increases learning performance in other insects (Roeder, 1999) it is likely involved in the formation of a neural nestmate recognition template. Thus, we suggest that the likely decrease of octopaminergic activity induced by social deprivation could mediate the need for trophallaxis but also lead to confusion in nestmate recognition.

In conclusion, worker–worker interactions are necessary to maintain a precise nestmate recognition level. Our results support that the template is mostly neural and has to be continually reinforced to maintain fine nestmate recognition capacities during the adult life. Although further experiments are necessary to determine the nature of these reinforcements (chemical or behavioural) emanating from nestmates, they could be mediated by an octopaminergic neural pathway. We also suggest that this and other examples of collective pattern emerging from individual interactions would be more systematically re-examined and may be integrated into the definition of eusociality.

## Acknowledgements

We would like to thank Dr Linda M. Hooper-Bui and Mr Jeff Murray from the Louisiana State University and Agricultural Center for their editorial and scientific comments.

## References

- Aarab, A., Jaisson, P., 1992. How to become a good ant-soldier: the effect of solicitation by minors on the development of aggressive behaviour in soldiers. *Anim. Behav.* 44, 593–595.
- Bhatkar, A.P., 1979a. Evidence of intercolonial food exchange in fire ants and other Myrmicinae using radioactive phosphorus. *Experientia* 35, 1172–1173.
- Bhatkar, A.P., 1979b. Trophallactic appeasement in ants from distant colonies. *Folia Entomol. Mex.* 41, 135–143.
- Boulay, R., Quagebeur, M., Godzinska, E.J., Lenoir, A., 1999. Social isolation in ants: Evidence of its impact on survivorship and behaviour in *Camponotus fellah* (Hymenoptera, Formicidae). *Sociobiology* 33, 111–124.
- Boulay, R., Hefetz, H., Soroker, V., Lenoir, A., 2000a. *Camponotus fellah* colony integration: worker individuality necessitates frequent hydrocarbon exchanges. *Anim. Behav.* 59, 1127–1133.
- Boulay, R., Soroker, V., Godzinska, E., Hefetz, A., Lenoir, A., 2000b. Octopamine reverses the isolation-induced increase in trophallaxis in the carpenter ant *Camponotus fellah*. *J. Exp. Biol.* 203, 513–520.
- Carlin, N.F., Hölldobler, B., 1986. The kin recognition system of carpenter ants (*Camponotus* spp.) I. Hierarchical cues in small colonies. *Behav. Ecol. Sociobiol.* 19, 123–134.
- Carlin, N.F., Hölldobler, B., Gladstein, D.S., 1987. The kin recognition system of carpenter ants (*Camponotus* spp.) III. Within-colony discrimination. *Behav. Ecol. Sociobiol.* 20, 219–227.
- Champalbert, A., Lachaud, J.P., 1990. Existence of a sensitive period during the ontogenesis of social behavior in a primitive ant. *Anim. Behav.* 39, 850–859.
- Cole, B.J., 1991a. Is animal behaviour chaotic? Evidence from the activity of ants. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 244, 253–259.
- Cole, B.J., 1991b. Short-term activity cycles in ants: generation of periodicity by worker interaction. *Am. Nat.* 137, 244–259.
- Crespi, B.J., Yanega, D., 1995. The definition of eusociality. *Behav. Ecol.* 6, 109–115.
- Dahbi, A., Lenoir, A., 1998. Nest separation and dynamics of the Gestalt odor in the polydomous ant *Cataglyphis iberica* (Hymenoptera, Formicidae). *Behavior. Ecol. Sociobiol.* 42, 349–355.
- Errard, C., 1986. Role of early experience in mixed-colony odor recognition in the ants *Manica rubida* and *Formica selysi*. *Ethology* 72, 243–249.

- Errard, C., Bagnères, A.-G., Lange, C., 1990. Change of the specific chemical signatures of two ants species reared in mixed colonies (*Formica selysi*, Formicinae and *Manica rubida*, Myrmicinae). In: Veeresh, G.K., Mallik, B., Virak-tamath, C.A. (Eds.), Social Insects and the Environment. New Delhi, Oxford & IBH Publ. Co. Pvt. Ltd, p. 408.
- Fresneau, D., Errard, C., 1994. L'identité coloniale et sa 'représentation' chez les fourmis. *Intellectica* 2, 91–115.
- Gordon, D.M., 1989. In: Harvey, P.H., Partidge, L. (Eds.), Caste and Change in Social Insects. Oxford University Press, Oxford, pp. 55–72.
- Gordon, D.M., 1996. The organization of work in social insect colonies. *Nature* 380, 121–124.
- Hefetz, A., Errard, C., Chambris, A., Le Negrate, A., 1996. Postpharyngeal gland secretion as a modifier of aggressive behavior in the myrmicine ant *Manica rubida*. *J. Insect. Behav.* 9, 709–717.
- Heinze, J., 1996. Reproductive hierarchies among workers of the slave making ant, *Chalepoxenus muellerianus*. *Ethology* 102, 117–127.
- Huang, Z., Plettner, E., Robinson, G.E., 1998. Effects of social environment and worker mandibular glands on endocrine-mediated behavioral development in honey bees. *J. Comp. Physiol. A* 183, 143–152.
- Huang, Z.-Y., Robinson, G.E., 1992. Honeybee colony integration: worker-worker interactions mediate hormonally regulated plasticity in division of labor. *Proc. Natl. Acad. Sci. USA* 89, 11726–11729.
- Huang, Z.-Y., Robinson, G.E., 1996. Regulation of honey bee division of labor by colony age demography. *Behav. Ecol. Sociobiol.* 39, 147–158.
- Jaisson, P., 1975. L'imprégnation dans l'ontogenèse des comportements de soins aux cocons chez la jeune fourmi rousse (*Formica polyctena* Först.). *Behaviour* 52, 1–37.
- Lahav, S., Soroker, V., Hefetz, A., Van der Meer, R.K., 1999. Direct behavioral evidence for hydrocarbons as ant recognition discriminators. *Naturwissenschaften* 86, 246–249.
- Lenoir, A., Fresneau, D., Errard, C., Hefetz, A., 1999. Individuality and colonial identity in ants: the emergence of the social representation concept. In: Detrain, C., Dendebourg, J.-L., Pasteels, J.M. (Eds.), *Information Processing in Social Insects*. Birkhauser Verlag, Basel Boston Berlin, pp. 219–237.
- Meskali, M., Bonavita-Cougourdan, A., Provost, E., Bagnères, A.-G., Dasticier, G., Clément, J.-L., 1995. Mechanism underlying cuticular hydrocarbon homogeneity in the ant *Camponotus vagus* (Scop.) (Hymenoptera: Formicidae): role of postpharyngeal glands. *J. Chem. Ecol.* 21, 1127–1148.
- Morel, L., 1983. Relation entre comportement agressif et privation sociale precoce chez les jeunes immatures de la fourmi *Camponotus vagus* Scop. (Hymenoptera: Formicidae). *C. R. Acad. Sci. Paris* 296, 449–452.
- Morel, L., Blum, M.S., 1988. Nestmate recognition in *Camponotus floridanus* callow worker ants: are sisters or nestmates recognized. *Anim. Behav.* 36, 718–725.
- Nielsen, J., Boomsma, J.J., Oldham, N.J., Petersen, H.C., Morgan, E.D., 1999. Colony-level and season-specific variation in cuticular hydrocarbon profiles of individual workers in the ant *Formica truncorum*. *Insect Soc.* 46, 58–65.
- Provost, E., Rivière, G., Roux, M., Morgan, E.D., Bagnères, A.-G., 1993. Change in the chemical signature of the ant *Leptothorax lichtensteini* Bondroit with time. *Insect Biochem. Mol. Biol.* 23, 945–957.
- Robinson, G.E., Heuser, L.M., LeConte, Y., Lenquette, F., Hollingworth, R.M., 1999. Neurochemicals aid bee nestmate recognition. *Nature* 399, 534–535.
- Roeder, T., 1999. Octopamine in invertebrates. *Prog. Neurobiol.* 59, 533–561.
- Sherman, P.W., Lacey, E.A., Reeve, H.K., Keller, L., 1994. The eusociality continuum. *Behav. Ecol.* 6, 102–108.
- Soroker, V., Fresneau, D., Hefetz, A., 1998. Formation of colony odor in ponerine ant *Pachycondyla apicalis*. *J. Chem. Ecol.* 24, 1077–1090.
- Soroker, V., Vienne, C., Hefetz, A., 1995. Hydrocarbon dynamics within and between nestmates in *Cataglyphis niger* (Hymenoptera: Formicidae). *J. Chem. Ecol.* 21, 365–378.
- Stuart, R.J., 1992. Nestmate recognition and the ontogeny of acceptability in the ant, *Leptothorax curvispinosus*. *Behav. Ecol. Sociobiol.* 30, 403–408.
- Van der Meer, R.K., Alonso, L.E., 1998. Pheromone directed behavior in ants. In: Van der Meer, R.K., Breed, M., Winston, M., Espelie, K.E. (Eds.), *Pheromone Communication in Social Insects*. Westview Press, Boulder, pp. 159–192.
- Van der Meer, R.K., Saliwanchik, D., Lavine, B., 1989. Temporal changes in colony cuticular hydrocarbon patterns of *Solenopsis invicta*: Implications for nestmate recognition. *J. Chem. Ecol.* 15, 2115–2125.
- Vienne, C., Soroker, V., Hefetz, A., 1994. Congruency of hydrocarbons patterns in heterospecific groups of ants: Transfer and/or biosynthesis. In: Lenoir, A., Arnold, G., Lepage, M. (Eds.), *Les Insectes Sociaux*. Université Paris Nord, Paris, p. 542.