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Interindividual Distances in Mixed-Species Groups of Ants: an Estimation of Cohesion in Social Groups

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Abstract — Spatial organization was estimated in mixed-species groups of ants with interindividual distance measures as a function of: (1) the age of the workers when associated; and (2) the presence of the brood. Workers of *Manica rubida* (Myrmicinae) and *Formica selysi* (Formicinae) were reared in single-species groups (control) or in artificial, mixed-species groups, created 5 h, 12 h or 22 h after emergence, with or without brood. By recording the location of each individual in the nest during the 10 days following the creation of the groups, we evaluated the spatial organization and the interindividual distances between homocolonial or allospecific workers, and between workers and homocolonial or allospecific brood. The cohesion of the group, depend on the age of the workers when associated: the younger the individuals are when the groups are created, the smaller are the interindividual distances. Moreover, homocolonial individuals aggregated with brood, when present, which improves the overall cohesion of the group. However, in mixed groups, both species associated preferentially with members of their own species. This suggests that newly-emerged ants do not depend totally on the odors of their nestmates to construct their recognition template and that they also possess an innate, specific template.

Ants societies are generally closed to non-nestmates but young workers can be adopted into alien, conspecific societies. A great number of studies have shown that the age of the workers influences the probability of being adopted. Very young individuals are better accepted than older ones. Many studies have demonstrated that young individuals have to be introduced into homospecific colonies immediately after their emergence (Wilson 1971). Jaisson (1972) suggested that the ability to transfer young workers from one colony to another could be partially explained by the presence of nymphal pheromones contained in the exuviae (see also Hölldobler & Michener 1980).

Research in various Formicinae belonging to the *Cataglyphis* and the *Camponotus* genus provides some information on the possibility of the adoption of young workers into alien, conspecific colonies (Carlin & Hölldobler 1986; Bonavita-Cougourdan et al. 1987; Clément et al. 1987; Lenoir et al. 1987; Morel & Vander Meer 1987; Morel et al. 1988; Stuart 1992). For example, workers of *C. cursor* only a few days old can be transferred to another colony and are neither attacked nor threatened, but individuals, 5 or more days old, are never accepted (Nowbahari & Lenoir 1989). This suggests that the adopted individuals acquire the factors necessary for recognition by the adoptive colony before developing their own specific signature or before their physiological maturation leads to aggressive behaviour.

Among social insects, workers are known to discriminate nestmates from non-nestmates (see reviews in Hölldobler & Michener 1980; Gadagker 1985; Breed & Bennett 1987) and it is generally agreed that nestmate recognition in ants, leading to preferential behaviour towards conspecifics, is mediated by chemical signals

(Howse 1975; Blum 1987).

These results concerned adoptions in conspecific colonies, so we used an artificially mixed group as an experimental structure, and tested social integration in these experimental mixed-species groups, to understand the mechanisms that occur in natural associations such as inquilines.

In an artificial mixed-species group (composed of different ant species belonging to the different subfamilies (Ponerinae, Myrmicinae, Pseudomyrmecinae, Formicinae and Dolichoderineae), Jaisson (1980), Errard (1984) and Errard & Jaisson (1984) have shown that the best-integrated mixed group can be obtained if the phyletic distance between the species is small and the workers are young.

It is thus possible to intervene earlier when the subject species are phylogenetically distant. We tested the "age" factor on the cohesion of 2 phylogenetically-distant species, *Manica rubida* (Myrmicinae) and *Formica selysi* (Formicinae) when creating artificial mixed-species groups. More specifically, we concentrated on finding out whether the age of the individuals when associated can influence the aggregation of both species of ants. Mixed colonies of these 2 species do not occur in nature, but, if these experimental conditions permit social integration, it seems plausible that they could also be involved in the formation of natural mixed colonies.

Attraction between nestmates and, consequently, the cohesion of the group could also depend on the queen (Berton et al. 1991), whose presence attracts workers. Hölldobler (1977) suggested that brood pheromones are also strongly attractive to the workers, and that this phenomenon obscures workers' responses to the specific odours of the colony. However, as no larval pheromone has been found, Morel and Vander Meer (1988) have suggested different hypotheses which might implicate larval behaviour toward nurses (review by Jaisson 1991). Cohesion in an artificially mixed colony has never been studied. So, we used interindividual distances to appreciate the cohesion of mixed-species groups. Interindividual distances in ants have previously been studied by Jaisson et al. (1991), who proposed that the average distance to the nearest neighbour within the nest might be considered as a phyletic index representative of cohesion level.

With these mixed-species groups, we investigated the influence of: (1) the age of the workers when placed in mixed-species groups; and (2) the presence of the brood (homocolonial or allospecific), on the spatial organization and the cohesion of the groups.

Since the chances of success in creating mixed-species groups depends on both the age of the individuals placed together as well as on the phylogenetic distance between them, our experimental model is only possible with workers having emerged less than 24 h earlier. All attempts at grouping *M. rubida* workers and *F. selysi* workers after they were 48 h old failed, with attacks leading to the rapid death of one or both species (Errard & Jallon 1987). Thus, in order to achieve the social integration of both species, we must associate workers during the tolerance period which lasts for one day after emergence.

In this way, it is possible to: (1) define the duration of the period of tolerance; (2) determine the point at which the 2 species will aggregate well as a function of the age of the individuals; and (3) analyse the effect of the brood on the worker cohesion.

Materials and Methods

Subjects and Rearing Conditions

Both species used, *Formica selysi* (Formicinae) and *Manica rubida* (Myrmicinae) were collected in Morillon (in the French Alps at an altitude of 700 m) in June 1984. Laboratory experiments were performed at 20±3℃ , with a natural photoperiod.

Each experimental group was reared in a test tube (180 mm×17 mm) fitted at one end with a water container (6 cm). Food (a honey/apple mixture and mealworms) was introduced through the other end which was closed with a cotton plug (2 cm), (Fig 1).

As soon as they emerged, young workers were selected and removed from their large mother colonies (1 colony per species) in order

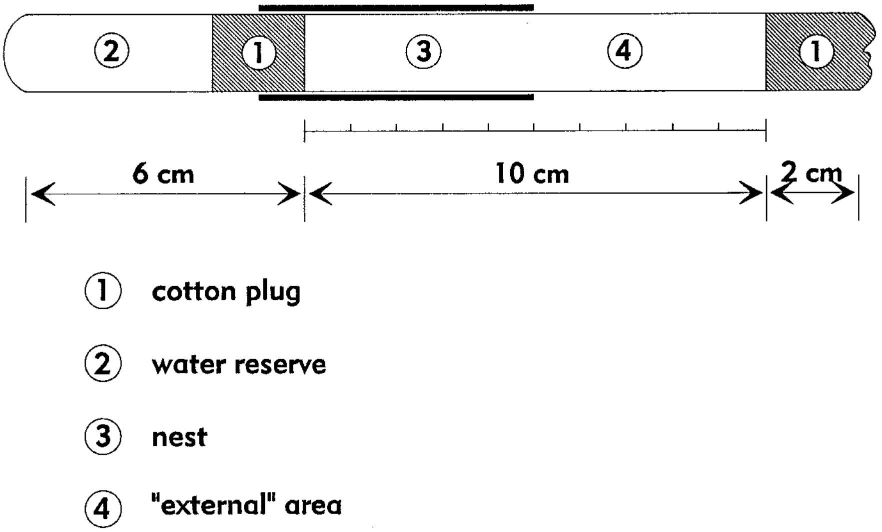

Fig. 1. Schema of the rearing tube (divided into 10 zones).

to create homocolonial control groups or heterospecific mixed groups. A control group contained 20–25 workers from a single species, while mixed group included 10–15 workers from each species. No group contained a queen, but some groups contained brood-10 cocoons (*F. selysi*) or 10 pupae (*M. rubida*)-from a single species.

Two experiments were carried out in order to test the influence of the: (1) age of the workers when placed in experimental groups; and (2) role of the brood.

In the first experiment, young workers from both species were reared in control or in mixed groups, created 5±1 h, 12±2 h or 22±2 h after their emergence. The mixed groups always included brood from a single species (either *F. selysi* cocoons or *M. rubida* pupae) and the control groups included homocolonial brood. For each age, a total of 8 mixed groups (4 with *F. selysi* cocoons, 4 with *M. rubida* pupae) and 4 control groups (2 *F. selysi* and 2 M. rubida) were created in this way.

In the second experiment, young workers 12±2 h old were selected in order to create mixed and control groups. Brood (*F. selysi* cocoons or *M. rubida* pupae) was added to a part of the mixed groups and to a part of the control groups. Twelve mixed groups (4 with *F. selysi* cocoons, 4 with *M. rubida* pupae and 4 without any brood) and 12 control groups (3 with homocolonial brood and 3 without any brood in each of *F. selysi* and *M. rubida*) were created in this way.

The brood added during the experiments was purposely selected at a very immature stage to avoid hatching during the tests.

Observations

Cohesion was assessed by recording the location of each worker and brood (spatial organization) in the rearing tube and by measuring the interindividual distances between homocolonial or allospecific workers, and between workers and homocolonial or allospecific brood.

The reported results were based on daily observations (1 per day per individual), conducted over 10 days following the constitution of the groups. In all types of associations, the spatial distribution began to be stable only 12 h after the creation of the groups, but it stayed stable for the 10 experimental days. The rearing tube was divided into 10 equal zones, of approximately 1 cm each. The location of each individual and of pupae or cocoon was recorded on a scale graduated from 1 (water reserve) to 10 (cotton plug). A computer programme (written on Apple 2e) used the location of each individual (worker and brood) for each species and gave the average interindividual distances in relation to the various rearing schemes. We supposed that each individual was in the middle of the zone; the average distances were calculated to the nearest number but remained fairly precise. When individuals were in the same zone, the interindividual distance was then ⌀. A series of frequencies indicating the presence of workers and brood in each of the 10 possible zones resulted in a spatial distribution profile for each species. The mean of the species frequencies (for the 10 days of observation) for each location yielded a group spatial distribution profile for each group.

Individuals of *F. selysi* were indicated by F, their brood by BF; individuals of *M. rubida* by M, and their brood by BM. The average distances calculated were either intraspecific (F/F, M/M, F/BF, M/BM) or interspecific (F/M, F/BM, M/BF). The results were analysed using variance analysis (ANOVA). The comparisons between different group spatial distributions were analysed using Chi-square analysis (χ^2).

Results

The Influence of the Age of the Workers When Associated

1) Group Spatial Distribution Profiles

When individuals were associated within the first few h after emergence, workers from both species gathered at the bottom of the tube, near the water reserve (zone 1) and tended to remain strongly aggregated (Fig. 2a). When 12 h old, the repartition of the workers was such that both species were found throughout the tube (Fig. 2b); this distribution became fairly homogenous when the mixed group was made up of 22-h-old individuals (Fig. 2c). The group spatial distribution profiles of the different age associations were significatively different in *M. rubida* and in *F. selysi* (χ^2=9.11, df=4, P<0.05).

2) Interindividual Distances

The mean distance between workers reared in mixed or in control groups increased in close relation to the age of the individuals when associated (Fig. 3). This was valid for the distance between homocolonial or allospecific individuals reared in mixed groups (F=76.70, df=2,159, P<0.001) (Fig. 3a), as well as between homocolonial individuals reared in control groups (F=35.74, df=2,79, P<0.001) (Fig. 3c).

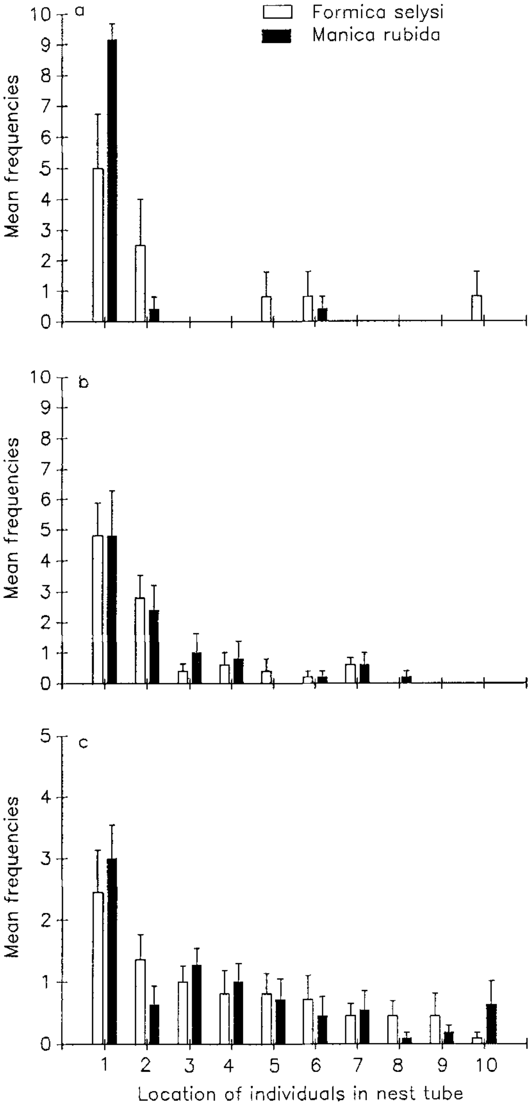

Fig. 2. Group spatial distribution profiles inside the rearing tube (graduated from 1 to 10) of *F. selysi* and *M. rubida* mixed worker groups, for different ages of association. (a) 5±1 h, (b) 12±2 h, (c) 22±2 h.

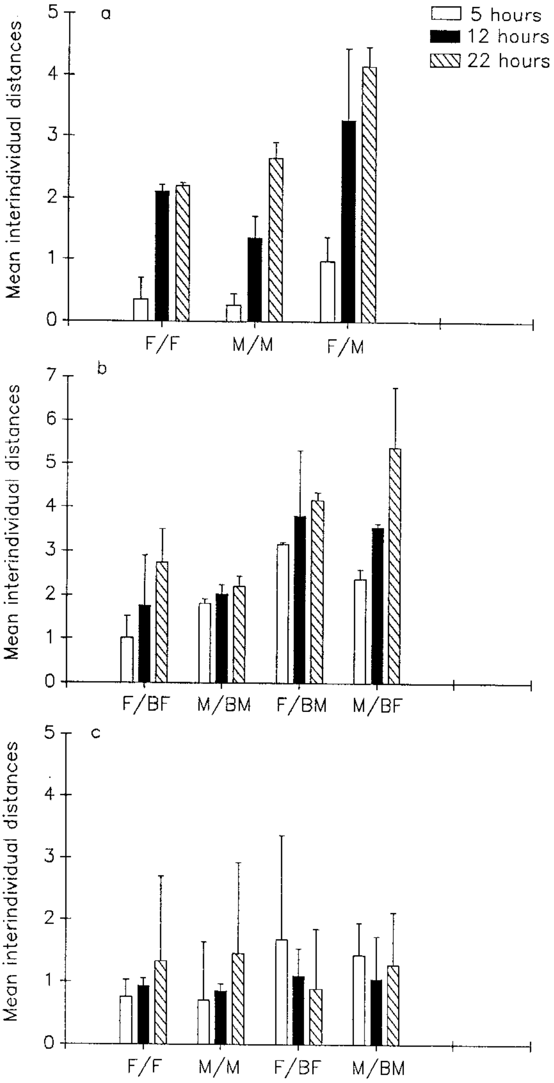

Fig. 3. Interindividual distances in *F. selysi* and *M. rubida* species, as a function of the workers' ages when associated (5±1 h, 12±2 h, 22±2 h): (a) intraspecific distances between *F. selysi* workers (F/F), *M. rubida* workers (M/M) and interspecific distances between the 2 workers species (F/M), when reared in mixed groups, (b) intraspecific distances between workers and homocolonial brood (F/BF, M/BM) and interspecific distances between workers and allospecific brood (F/BM, M/BF), when reared in mixed groups. (c) intraspecific distances between workers (F/F, M/M), between workers and homocolonial brood (F/BF, M/BM), reared in control groups.

In mixed groups, the distances between workers and homocolonial or allospecific brood were also smaller when 5-h-old individuals were associated than when 12-h- or 22-h-old individuals were associated (F=36.33, df=2,159, P<0.001) (Fig. 3b). In contrast, when workers were reared in control groups, the interindividual distances between workers and brood not vary with age of the workers when associated (F=7.41, df=2,79, N.S.) (Fig. 3c).

When the 2 species were associated 5 h after emergence, group cohesion was very strong, with the inter- and intraspecific interindividual distances means reaching a maximum of 1 cm. When 12-h-old individuals were associated, both the intraspecific interindividual distances (1.5 – 2 cm) as well as interspecific distance (3 cm) increased. Finally, when 22-h-old individuals were associated, they remained very distant from both homocolonials (2 – 3 cm) and allospecifics (4 cm), (intraspecific distances: F=39.90, df=2,79, P<0.001; interspecific distances: F=55.86, df=2,79, P<0.001). Whatever the age of the individuals when placed together, the intraspecific interindividual distance is always inferior to the interspecific distance (F=58.31, df=1,79, P<0.001). The same phenomenon was observed for the distances between individuals and brood, the distance between the individuals and the homocolonial brood always being lower than the distance between workers and allospecific brood (F=53.39, df=1,79, P<0.001). When the associations were created with workers 12-h- or 22-h-old, the intraspecific distances were significantly lower in control groups than in mixed groups (F=57.30, df=1,79, P<0.001). However, no difference appeared for 5-h-old workers.

Influence of the Presence of the Brood

1) Group Spatial Distribution Profiles

Without any brood, both species were distributed throughout the tube, however, their numbers were greater near the water reserve (Fig. 4a). There was no significant difference between the spatial distribution profiles of *M. rubida* and *F. selysi* workers (χ^2=0.34, df=8, N.S.).

When brood was present in mixed groups, *M. rubida* pupae were concentrated in zones near the water reserve (1 – 2 – 3) (Fig. 4b), whereas

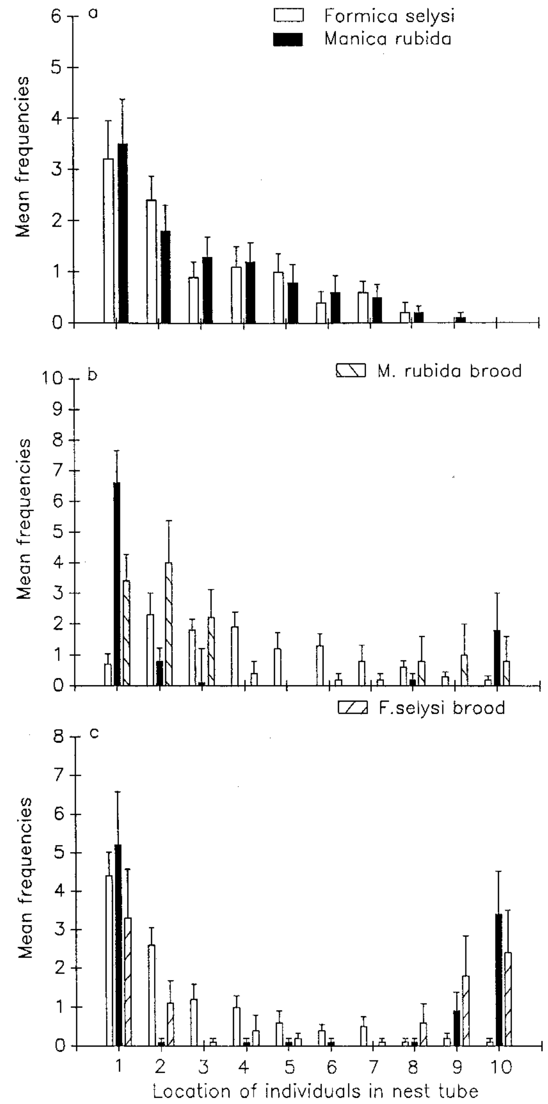

Fig. 4. Group spatial distribution profiles inside the rearing tube of *F. selysi* and *M. rubida* workers and brood when reared in mixed groups with or without brood. (a) without brood, (b) with *M. rubida* pupae, (c) with *F. selysi* cocoons.

F. selysi cocoons were distributed near the water reserve (1–2), but also near the cotton plug (9–10) (Fig. 4c). However, between the spatial distribution profiles of both species we did not observe any statistical difference (χ^2=4.74, df=9, N.S.).

The worker distribution profiles in mixed groups as a function of the homocolonial brood showed that *M. rubida* or *F. selysi* workers gathered in Zone 1, near their brood. However, *M. rubida* workers tend to aggregate their brood much more than *F. selysi* workers. In this case, the distribution profiles of *M. rubida* workers were different with and without brood, and workers gathered close to the brood (Fig. 4ab) (χ^2=5.62, df=2, P<0.05). The placement of *F. selysi* workers was very similar with or without brood (Fig. 4ac) (χ^2=0.39, df=2, N.S.).

The worker distribution profiles in mixed groups as a function of the allospecific brood (Fig. 4bc) showed that *M. rubida* were no affected by the species of the brood, gathering near allospecific cocoons as well as homocolonial pupae (χ^2=1.37, df=2, N.S.). *F. selysi* workers were distributed throughout the tube, but did not cohabit with the allospecific pupae as with homocolonial cocoons (χ^2=2.91, df=2, N.S.).

2) Interindividual Distances

The mean distance between workers and their brood was always smaller than that between workers and the allospecific brood (F=6.92, df=1,39, P<0.001). The mean interindividual distance between individuals and homocolonial brood was also larger in mixed groups than in control groups (F=2.40, df=1,39, P<0.02 in *F. selysi*; F=3.90, df=1,39, P<0.005 in *M. rubida*) (Fig. 5a).

When brood was present, *M. rubida* individuals tended to aggregate near their brood, which resulted in a reduction in the intraspecific interindividual distance (F=40.43, df=1,39, P<0.001). In contrast, the intraspecific distance of *F. selysi* workers did not vary in terms of the presence of its brood (F=1.40, df=1,39, N.S.), nor did the interspecific interindividual distances vary, with or without the presence of brood (F=1.69, df=1,79, N.S.) (Fig. 5b).

The interindividual distances in control groups without brood were always larger than the interindividual distances in groups with brood, whatever the species (F=110.57, df=1,119, P<0.001) (Fig. 5b).

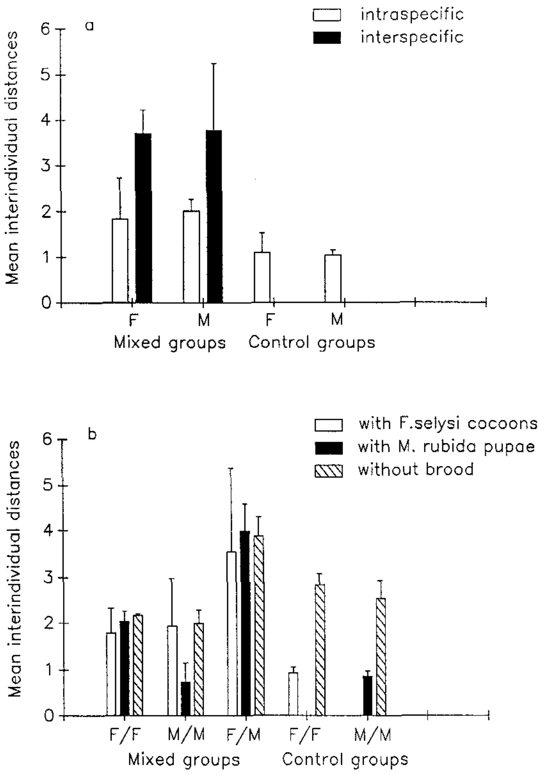

Fig. 5. Interindividual distances in *F. selysi* and *M. rubida* species reared in mixed and in control groups, (a) intraspecific and interspecific distances between workers of *F. selysi* (F) or *M. rubida* (M), and homocolonial brood or allospecific brood, (b) intraspecific (F/F, M/M), and interspecific (F/M) distances between workers, as a function of the brood's presence, with *M. rubida* pupae, with *F. selysi* cocoons or without brood.

Discussion

These results confirm those obtained from studies on the attractivity of the brood (Fresneau et al. 1989; review by Hölldobler & Wilson 1990). In mixed-species groups, the spatial distribution inside the nest tube appears to be similar to the previous data concerning groups spatial distribution (Corbara & Errard 1991). *M. rubida* workers group their brood and aggregate around it, whereas *F. selysi* workers as their cocoons tend to be more scattered throughout the tube nest. Within a mixed group, *M. rubida* workers may produce much more brood directed behaviour than do *F. selysi* workers.

In mixed groups containing an association of *F. selysi* and *M. rubida*, we have shown that the presence of homocolonial as well as allospecific brood in a group allows *M. rubida* individuals to aggregate with it, improving the cohesion of the group. *F. selysi* workers are spread throughout the nest and never cohabit with the allospecific brood, as already shown by Corbara & Errard (1991).

It also appears that the social integration of both species and, consequently, the cohesion of the group, depend on the age of the individuals. The younger the individuals are when the groups are made up, the smaller the interindividual distances. These results and the fact that mixed groups are not possible with individuals older than 24 h, confirm the existence of a transitory period of tolerance during the first 24 h after emergence in which preferential relations between individuals from the 2 species can be established. The integration of the 2 species seems therefore easier to obtain when the workers are younger (5-h-old). However, even if workers are associated as soon as they emerge, the interindividual distances always remain larger in mixed-species groups than in single-species groups, which shows that cohabitation between the 2 species is not as perfect as that within the same species. When forced to live in a heterospecific group, young *F. selysi* and *M. rubida* workers do not display reciprocal aggressivity, and even demonstrate limited social interactions (Corbara & Errard 1991). These results show the existence of a direct relationship between the level of social interactions and interindividual distances.

It is known that many kinds of animals observe a more or less precise interindividual distance that is species-specific (see Wilson 1975; Jaisson et al. 1991). As in other social insects, ants belonging to the same nest have a universal tendency to aggregate under natural conditions. Thus, if a group of workers is taken away from its nest and put into neutral arena, most of the individuals reassemble. Workers might reassemble according to the dioxyde gradient (produced by the group of ants) as in *Solenopsis* (Wilson 1962; Hantgartner 1969). Pheromones may also be involved in the phenomenon of the aggregation of individuals. For example, Ayre and Blum (1971) demonstrated that, in different *Camponotus* species, small amounts of a secretion from the Dufour gland are very attractive to the workers. A similar response has been recorded in *Oecophylla longinoda* with secretions from the sternal gland (Hölldobler & Wilson 1977). In this case, the pheromone acts as a recruiting signal and prompts the aggregation of nestmates. Recently, Snyder (1993) showed cases in a colony of *Formica argentea* where workers directed preferential behaviour towards particular subgroups. This may have been a consequence of task specialization among subgroups or may have lead to aggregations of super-sisters at specific sites.

In mixed societies, the interindividual distance seems to be the compromise between attraction and repulsion, which is different between homocolonial and heterospecific workers.

The apparent chemical basis for this peaceful co-inhabitancy is the ability of members of such mixed-species groups to adopt a unified chemical signature (Bagnères et al. 1991). In fact, further studies demonstrated that in mixed-species groups, workers of *F. selysi* and *M. rubida* acquired some of the characteristic hydrocarbons of their heterospecific nestmates over the course of a few hours (Errard & Jaisson 1991; Errard 1994a). These qualitative changes in the chemical profile of each species probably permitted both species to cohabit (interindividual distances decrease) and display amicable behaviour. This presumed function is also corroborated by chemical similarity of cuticular hydrocarbon profiles of termitophile (Howard et al. 1980) and myrmecophile insects (Vander Meer & Vojcik 1982). However, in all of our experimental studies, the 2 species aggregated preferentially with members of their own species. The interspecific distances were always larger than intraspecific distances, despite the fact that from a chemical viewpoint a "mixed group odour" had been identified. In all cases, specific recognition remains a priority: workers prefer conspecifics.

In ants, the recognition of the homocolonial or conspecific chemical signature may be learned before or just after emergence (Isingrini et al. 1985); allospecific chemical signatures might also be learned during this sensitive period (Morel et al. 1988; Errard 1994b). This period is therefore important for the elaboration of recognition criteria and for the acceptance or rejection of partners (Jaisson 1975). In many social insects, early experience may induce a tolerance for a particular social environment and may explain the natural associations between different species of ants. The existence of these imprinting-like phenomena allows newly emerged workers to become well integrated in an alien colony. This hypothesis is supported by studies of slavemaking ant species (Bushinger et al. 1980, Le Moli & Moli 1985).

The results suggest a strong environmental influence on the recognition of nestmates. The template of newly emerged individuals would be flexible enough to be influenced by allospecific odours during a short sensible period after emergence. However, young ants are not totally dependant on their environmental odours and possess an innate, specific template which prevails, in spite of the spatial proximity between individuals during their early life.

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