

Spatial Organization & Nestmate Recognition in Artificial Mixed Colonies of *Manica rubida* and *Myrmica rubra* (Hymenoptera: Formicidae)

by

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ABSTRACT

We studied nestmate recognition in artificially mixed colonies of the closely related ants *Manica rubida* and *Myrmica rubra* (Myrmicinae). We have recorded the spatial partitioning of individuals and brood in different colonies: homospecific control colonies and heterospecific experimental colonies (mixed colonies containing workers of both species with either a *M. rubida* or a *M. rubra* queen). The degree of recognition between individuals was quantified by aggression tests. As contrasted to mixed colonies composed of species belonging to different subfamilies, which simply co-exist, this pairing of related species results in integration of the two species with interspecific altruistic relationships and without aggression. *Manica* queens affect nestmate odor and *Myrmica* workers' behavior more than do *Myrmica* queens. *Myrmica* is more tolerant of allospecific individuals to whom submission behavior is often directed. This species adapts itself to the presence of *Manica* individuals. These results could be due to the differences of the queens' size or of the degree of polygyny between the two species.

KEY WORDS: Formicidae, nestmate recognition, mixed colony, polygyny, spatial organization.

INTRODUCTION

It has been known for more than a century that all individuals foreign to ant colonies are attacked and driven out (Forel, 1874; Fielde, 1904; Le Masne, 1952). However, colonies containing two

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species, and occasionally more, are not uncommon.

In this way, individuals use olfactory cues to discriminate nestmates from non-nestmates (Wilson, 1971). Indeed, each individual has an odor, and these odors are learned to be recognized by each member of the colony.

This odor can theoretically originate from different sources: environmental factors (i.e. diet, material of the nest), genetic factors produced by workers and factors transferred to workers from the queen.

The contribution of the queen in nestmate recognition cues is variable according species. Its importance has been demonstrated i.e. in small colonies of *Camponotus* (Carlin and Hölldobler, 1986), in *Leptothorax lichtensteini* (Provost, 1989). In the other hand, it seems that the queen is not an important source for recognition cues in some Leptothoracinae (Stuart, 1987), in *Pseudomyrmex ferruginea* (Mintzer, 1982), and in *Solenopsis invicta* (Obin and Vander Meer, 1989). Hölldobler and Michener (1980) have suggested that the queen should contribute most to colony odor in monogyne species.

Experimental mixed colonies containing several species that do not naturally form heterospecific associations have been studied by several authors (Forel, 1874; Fielde, 1903; Errard & Jaisson, 1984; Errard, 1984, 1986; Corbara & Errard, 1990). By modifying the early environment of individuals, experimental heterospecific colonies provide a system in which the post-emergence recognition signals between individuals can be studied.

For our experiments, we selected *Manica rubida* and *Myrmica rubra* and mixed larvae of each species together under an allo- or conspecific adoptive queen. We chose these two species and mixed them at the larval stage because the probability of successfully establishing heterospecific colonies increases the more closely related the species used and the earlier they are combined (Jaisson, 1980; Errard, 1984; Errard & Jaisson, 1984). *Manica rubida* and *Myrmica rubra* are phyletically close, both belonging to the subfamily Myrmicinae and they were for a long time classified in the same genus. They differ mainly in their degree of polygyny which is greater in *M. rubra*. On average there is one queen for every 100 workers but in extreme cases there may be one for every 30 workers (Cammaerts, 1989). In *M. rubida*,

there are only a few queens for many thousands of workers (we speak in this case of oligogyny).

This study was conducted to look for several points:

- 1) the spatial organization of individuals in these different colonies (homospecific and heterospecific)
- 2) the nestmate recognition between individuals reared in social environments, which differ by the queen's species
- 3) Given Hölldobler and Wilson's observations (1977) that species with a high degree of polygyny are more tolerant to unknown conspecifics, it was of interest to seek a confirmation in the case of meetings with allospecific individuals.

MATERIAL AND METHODS

Myrmica rubra were collected in April 1987 near Tours (France). *Manica rubida* colonies came from 800m above sea level in the French Alps and were collected in July 1987. *Myrmica* queens were separated from their original colonies and placed individually in glass housing tubes. *Manica* queens (being foundresses without workers) were placed in identical tubes. Eggs, larvae and pupae were removed from the original colonies. Brood from the two species, which could be distinguished by the size and shape of the larvae, were mixed and put into the laboratory nests. The success of this adoption procedure was variable but, in most cases, repeated presentation of heterospecific broods eventually resulted in acceptance. Two kinds of heterospecific colony were produced, two with *M. rubida* and *M. rubra* workers and a *M. rubida* queen, and three with both species of workers and a *M. rubra* queen. Four homospecific control colonies were produced by isolating single queens from the original colonies in laboratory nests. Brood from the same original colonies were then added to each nest to yield colonies of the same size as the heterospecific ones.

All the colonies were maintained under the same conditions: temperature of $22\pm 3^{\circ}\text{C}$, natural photoperiod of Paris, and a constant humidity. Mealworm larvae and a mixture of honey and apple were provided as food.

The mixed and control colonies were studied following one month in the stable housing conditions, the number of workers of both species being equal. We recorded the localization of individuals

and brood between October and December 1987; the average age of the workers was one month. Four scans per day were carried out with a mobile binocular lens in red light, yielding four observations per individual each day. The nests were divided into six sections, numbered from 0 to 5, with 0 corresponding to the foraging area. The ants were not individually identified, but their small number eliminated the danger of recording the same ant twice during observations.

The mixed colonies contained a mean of four larvae of each species which could be distinguished on the basis of differential morphology. Measurements were made for each of the following colonies:

- 2 control *Myrmica* colonies, each containing 6 workers, 1 queen and 8 larvae.
- 2 control *Manica* colonies, each containing 8 workers, 1 queen and 8 larvae.
- 2 mixed colonies with a *Manica* queen containing 6 workers (3 of each species) and 4 larvae of each species.
- 3 mixed colonies with a *Myrmica* queen, two of which contained 6 workers (3 of each species) and one with 16 workers (8 of each species). All three contained 4 larvae of each species.

The results are presented as frequencies in each of the nest chamber relative to the 30 location measurements. It was verified that results were not different between colonies, so the data were lumped together to give a single distribution for each type of colony. The distributions for the different colony types were compared with the χ^2 test using observed frequencies.

In order to estimate the recognition between ants of the control and mixed colonies, we used tests of aggressiveness in a neutral arena consisting of a 4.8 cm diameter Petri dish, after seven to eight months of association. Two ants from different colony are placed together and agonistic interactions were recorded for each ant every five second over five minutes. These interactions were divided into: Threats (T) (mandible opening and gaster flexing), Attacks (A) (bites, stings, or carrying and dragging), Submissions (S). All of these agonistic interactions have been described by De Vroey (1978). In her tests, the worker considered

as the intruder displayed submissive behaviors. This is a widespread behavioral response shown by aggressed animals because of the well-known importance of movement as a trigger for attack. This posture is thus in fact an appeasement behavior. Six series, each of 20 tests, were carried out with individuals from the different colonies. The results for each series are presented as histograms showing the median frequency of each agonistic behavior. Data for different categories were compared using Wilcoxon test.

RESULTS

1. Spatial distribution of ants and brood.

1. In control colonies (Fig. 1).

The *Myrmica* workers mostly remain grouped near to the queen and the brood (χ^2 NS), and rarely leave the nest (Fig. 1a).

The *Manica* workers are more dispersed than the *Myrmica* ($\chi^2=221$, $p<0.001$), leave the brood ($\chi^2=197$, $p<0.001$) and the queen ($\chi^2=20.22$, $p<0.001$) (Fig. 1b). Observations showed that they move more than *Myrmica* workers and they are more frequently outside the nest.

The queens of the two species remain with the brood in a single nest chamber over 96% of the time.

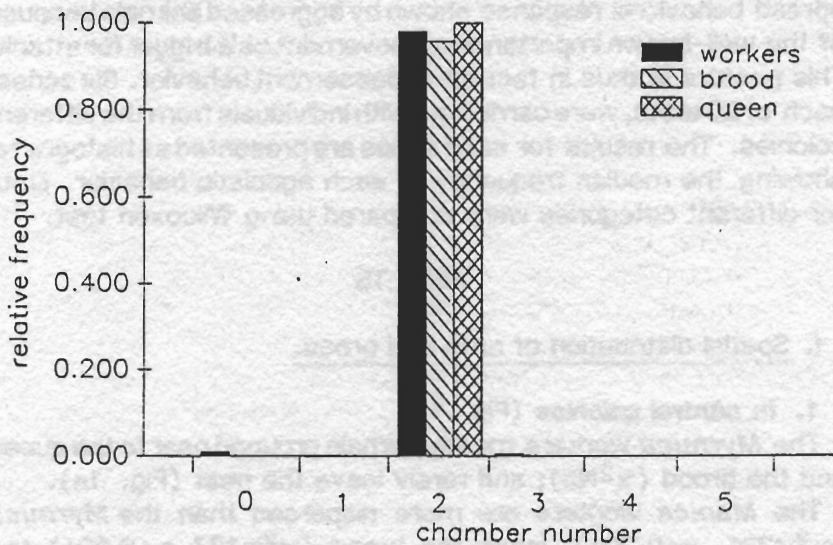
2. In heterospecific colonies with a *M. rubra* queen (Fig. 2a).

Compared to the *M. rubra* control colonies, the distribution of the different elements considered here (queen, workers and brood) is much less concentrated in a specific chamber (respectively $\chi^2=74.11$, $p<0.001$; $\chi^2=214.76$, $p<0.001$; $\chi^2=338.11$, $p<0.001$).

This disruption is no doubt due to *Manica* workers which are more mobile. They move the brood, which also induces movement of the queen which is found in chamber 1 only 68% of the time, and in chamber 5, 25%, resulting in a spatial disorganisation of the colony.

The queen is always found with allo- and conspecific brood (χ^2 NS), attracting workers of its own species (χ^2 NS), which are more centered on conspecific (χ^2 NS) than on allospecific larvae ($\chi^2=28.07$, $p<0.001$). She does not, however, influence the *Manica* workers which remain divided up in several nest chambers

a. MYRMICA CONTROL COLONIES



b. MANICA CONTROL COLONIES

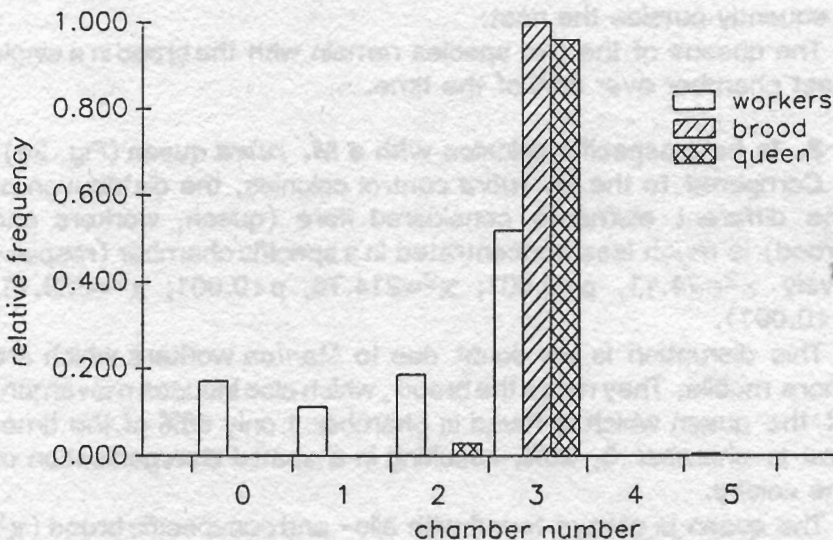


Fig. 1. Histograms of spatial partitioning in control homospecific colonies.

Fig. 1. Histogrammes de la répartition spatiale en colonies témoins homospecifics.

(compared to the queen $\chi^2=6.82$, $p<0.05$; compared to *Myrmica* workers $\chi^2=13.49$, $p<0.005$), with a significantly different distribution from the brood ($p<0.001$). The difference that is also noted for the distribution of the workers of the two species ($\chi^2=13.49$, $p<0.001$) can be largely explained by the fact that the *Manica* have a higher level of outside activities.

3. In heterospecific colonies with a *M. rubida* queen (Fig. 2b)

As before, the distribution of the different elements is more heterogenous than with the control colonies: $\chi^2=45.43$, $p<0.001$ for the queen; $\chi^2=107.38$, $p<0.001$ for the workers; $\chi^2=454$, $p<0.001$ for the brood.

The *Manica* queen is found in more chambers (primarily three) than the *Myrmica* queen (found in two) in the previous colonies ($\chi^2=30.17$, $p<0.001$). She attracts workers of both species who have a similar distribution to herself (χ^2 NS). The queen therefore appears to have a greater influence on the allospecific workers than does the *Myrmica* queen. However, the queen concentrates her activity more on her own brood (χ^2 NS) than on the allospecific brood ($\chi^2=9.60$, $p<0.005$). It could be noted that the workers of both species remain away from both allo- and conspecific larvae ($p<0.001$ for the four conditions). The *Myrmica* are thus no longer as close to the conspecific brood as they were in mixed colonies with a queen of their own species.

In this case, the different distribution of the two species of workers ($\chi^2=14.62$, $p<0.05$) may be explained by the higher level of outside activities found in *Manica*.

II. Study of interspecific aggressiveness.

1. Agonistic interspecific interactions of individuals from control colonies (Fig. 3a).

This test reveals aggression with threats and attacks, without significant difference between the two species. The submission behavior is only seen when *Myrmica* is confronted with a *Manica*. This behavior therefore is important because it represents the main difference between our two species. It is not observed in homospecific encounters of *Myrmica*, whereas we have seen it in confrontations between control *Myrmica* and *Myrmica* from mixed colonies with a *Myrmica* queen (unpublished observations).

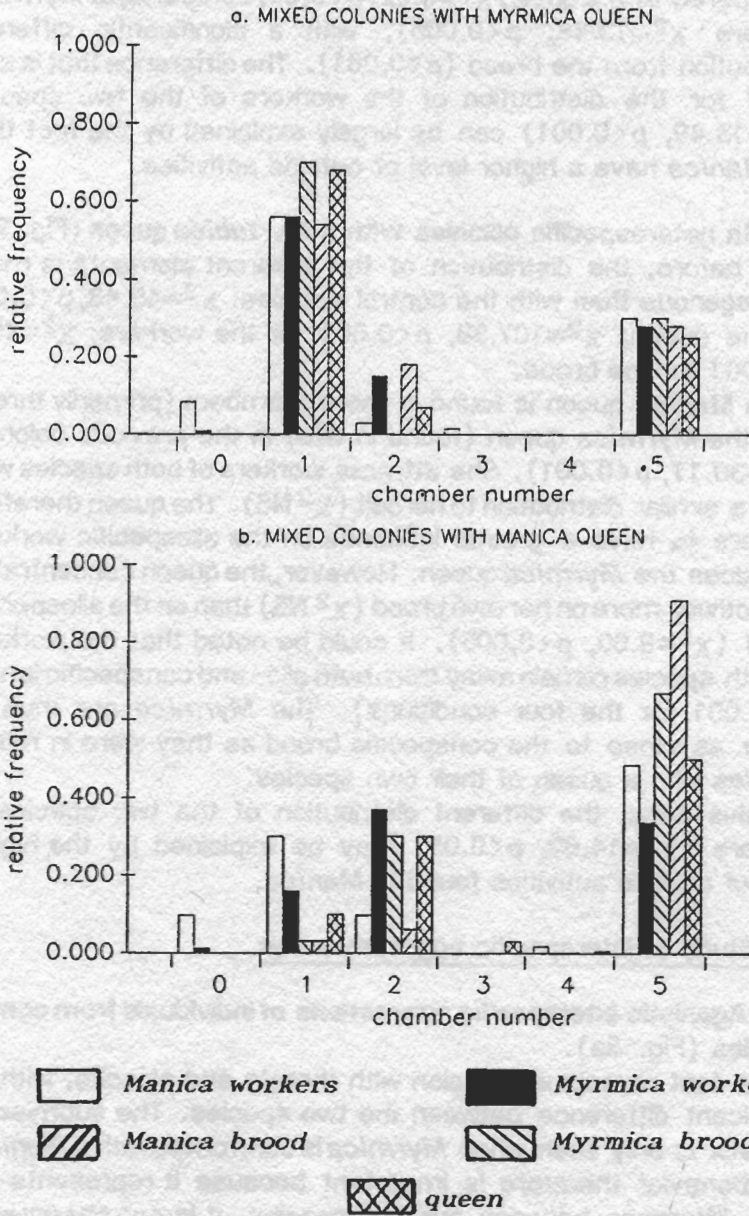


Fig. 2. Histograms of spatial partitioning in heterospecific colonies.
 Fig. 2. Histogrammes de la répartition spatiale en colonies heterospécifiques.

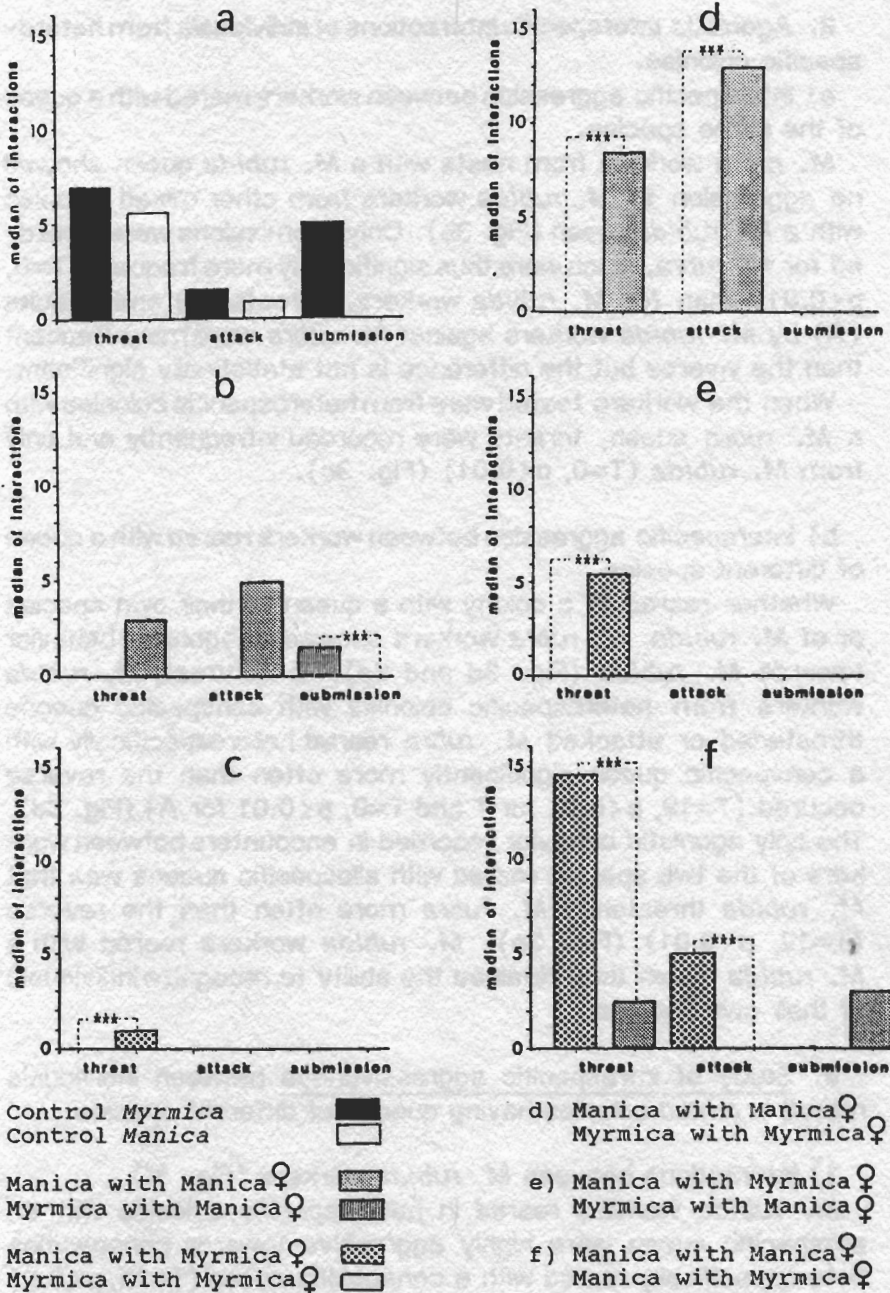


Fig. 3. Median of agonistic interactions on 20 tests between workers. T Wilcoxon (two-tailed): *** p<0.01

Fig. 3. Médiane des interactions agonistiques sur 20 tests entre ouvrières. T Wilcoxon (bilatéral): ***p<0.01

2. Agonistic interspecific interactions of individuals from hetero-specific colonies.

a) Interspecific aggression between workers reared with a queen of the same species.

M. rubra workers from nests with a *M. rubida* queen showed no aggression to *M. rubida* workers from other mixed colonies with a *M. rubida* queen (Fig. 3b). Only submissions were recorded for *M. rubra*, which were thus significantly more frequent ($T=0$, $p<0.01$) than for *M. rubida* workers. Threats (T) and attacks (A) by *M. rubida* workers against *M. rubra* were more frequent than the inverse but the difference is not statistically significant.

When the workers tested were from heterospecific colonies with a *M. rubra* queen, threats were recorded infrequently and only from *M. rubida* ($T=0$, $p<0.01$) (Fig. 3c).

b) Interspecific aggression between workers reared with a queen of different species.

Whether reared in a colony with a queen of their own species or of *M. rubida*, *M. rubra* workers showed no agonistic behavior towards *M. rubida* (Fig. 3d and 3e). In contrast, *M. rubida* workers from heterospecific colonies with conspecific queens threatened or attacked *M. rubra* reared heterospecifically with a conspecific queen significantly more often than the reverse occurred ($T=19$, $p<0.01$ for T and $T=0$, $p<0.01$ for A) (Fig. 3d). The only agonistic behavior recorded in encounters between workers of the two species reared with allospecific queens was that *M. rubida* threatened *M. rubra* more often than the reverse ($T=12$, $p<0.01$) (Fig. 3e). *M. rubida* workers reared with a *M. rubida* queen thus retained the ability to recognize individuals of their own species.

III. Study of intraspecific aggressiveness between individuals reared in mixed colonies having queens of different species.

1) Interactions between *M. rubida* workers (Fig. 3f)

M. rubida workers reared in heterospecific colonies with an allospecific queen were highly aggressive towards conspecifics heterospecifically reared with a conspecific queen ($T=15$, $p<0.01$ for T and $T=9$, $p<0.01$ for A). We have observed submission behavior for these latter (NS) and for the first time for *Manica*

in our tests, which confirms that individuals of the same species but reared in different social conditions do not recognize each other.

2) Interactions between *M. rubra* workers.

M. rubra workers showed no agonistic behavior irrespective of the species of queen with which they were reared (no figure).

DISCUSSION

Our results indicate that interspecific adoptions of brood results in more than mutual tolerance between the species involved. In contrast to Corbara and Errard observations (1989 and 1990) concerning mixed colonies comprising two species belonging to different subfamilies, *Formica selysi* and *Manica rubida* that each conserves its species-specific spatial and social characteristics, those results yield a true fusion of the two species. The species do not merely coexist in the same nest. Heterospecific colonies showed a spatial reorganization that leads to an integration between both types of individuals living in the same chambers of the colony, and no agonistic interactions were recorded within the experimental, mixed species, colonies. Furthermore, there was also a social reorganization illustrating the fact that this association is more than a simple cohabitation, since we observed interspecific altruism in the form of brood care, mutual grooming and trophallaxis.

However, in these mixed colonies, our observations have shown that *Myrmica* individuals are more involved in heterospecific behavior than *Manica* ones, which conserve their species-specific behavior; the queens increase the heterospecific activities of allo-specific workers, the influence of *Manica* queens being more evident (Vienne and Errard, 1989; Errard *et al.*, 1990).

Heterospecifically reared, *Manica* preserve their partitioning in several chambers of the nest like in homospecific colonies. Even with a *Myrmica* queen, their partitioning is significantly different from foreign individuals (queen and workers) and foreign brood. *Myrmica* workers take the same partitioning that *Manica* does, in contrast to the control colonies (they spend in this last case, almost 100% of their time in only one chamber with the queen and the brood).

Furthermore, in the presence of *Manica* queen, *Myrmica* workers are not so close to their own brood. Thus, it appears that the *Manica* queen influences more allospecific workers than the *Myrmica* queen does.

The study of agonistic interactions suggests that *Manica* queens affect nestmate odor more than do *Myrmica* queens.

In heterospecific encounters, there are more significant agonistic interactions when the two confronted individuals are reared with a queen of a different species. Moreover, *Manica* workers are more aggressive towards those of *Myrmica*, especially when they are reared with a conspecific queen. This phenomenon does not exist for *Myrmica* workers which display no agonistic interactions irrespective of the species of the queen with which they were reared. This appears also in homospecific encounters between ants reared in different type of mixed colonies: *Myrmica* do not recognize the others as non-nestmates, in contrast to *Manica* which hardly fight.

A number of explanations may be proposed for these differences. First, the fact that the *Manica* queens were foundresses (as opposed to the *Myrmica* queens) was probably not of fundamental significance, because the brood given for adoption came from mature colonies thereby yielding normal-sized workers (Wood and Tschinkel, 1981) and not dwarf workers that have a different behavior adapted to the foundation of a colony (Porter and Tschinkel, 1986).

On the other hand, it is possible that the queens' size may have affected workers' behavior. Indeed, the *Manica* queens are bigger than the *Myrmica* (medium weight of a *Manica* queen: $16.45\text{mg} \pm 2.4$; for a *Myrmica* queen: $4.28\text{mg} \pm 1.16$), which implies that their influence within the colonies could be more obvious. They provide a greater surface area for workers to contact which could imprint the queen's specific odor. The components of chemical signature in the cuticle of the two species were determined using gas chromatography coupled with mass spectrometry. The first results show that the queen would stimulate the appearance of its species specific hydrocarbons in allospecific workers; it seems also that this phenomenon is greater (about twice) from *Manica* queen than from *Myrmica* ones (Vienne *et al.*, 1990). We are currently preparing mixed colonies with two *Myrmica* queens in order to verify this hypothesis.

These differences could also be linked to the variable degree of polygyny found in these two species. Monogynous species are less tolerant of conspecific individuals from other colonies than are polygynous species (Hölldobler and Wilson, 1977). More recently, experiments in which alien workers of *Messor barbarus* were transferred between monogynous and polygynous colonies showed that the latter had a lower degree of closure (Cerdan and Provost, 1990). Our data suggest that the relationship can also be applied among polygynous species. Indeed, in all of our tests, the *Myrmica* reared in mixed colonies display almost no agonistic behavior, but only submissions to *Manica* coming from mixed colonies with a *Manica* queen.

Thus, a positive correlation between the opening of societies and the degree of polygyny of the considered species could exist. Le Roux (1980) showed that foreign individuals (of the same or different species) may easily be accepted into *Myrmica rubra* colonies (polygynous) at various developmental stages. This contrasts to *Myrmica ruginodis* (monogynous species) which reject any individual not having emerged within their colony.

Another explanation could be that the same relation would exist between the degree of polygyny and the species' behavioral plasticity. The large number of queens in a polygynous colony ensures that the average relatedness of workers is very low. Pearson (1983) found that intra-colonial levels of genetic relatedness among workers in *Myrmica rubra* was not significantly different from zero. Workers, therefore, care for brood and interact with individuals to which they are not necessarily related. Polygynous species may well have evolved a disposition to care for, or accept, genetically unrelated individuals.

In our experiments, the highly polygynous *M. rubra* was more tolerant of the other species. It appears therefore that *M. rubra* is influenced more easily than *M. rubida* by the conditions under which early learning occurred. *M. rubida* seems less affected by conditions encountered in early life. It retains its species specific behavior when reared heterospecifically.

The results of spatial, behavioral and chemical studies show a correlation between the degree of polygyny and the behavioral plasticity for the species *Myrmica rubra* and *Manica rubida*: the more polygynous a species, therefore, the more plastic its

behavior. Increased variability among individuals increases the overall capacity of a colony to adjust to new social conditions. This rule may be valuable for Myrmicinae as all Formicinae seem to be very plastic, either polygynous or monogynous (Jaisson, 1985).

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