

Species polyethism in heterospecific groups of Myrmicinae ants

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We studied species polyethism in heterospecific queenless and queenright groups of ants by associating *Manica rubida* (olygogynous) individuals with *Myrmica rubra* (polygynous) and *Myrmica ruginodis* (monogynous) individuals, respectively. In queenless and queenright groups, *Myrmica* workers specialized in brood care and guarding the nest while *Manica* workers performed activities normally reserved for the oldest workers (especially outside activities). This might be due to a more rapid ethogenesis in workers of the genus *Manica*. *Myrmica* workers appeared more plastic in their behaviour and more sensitive to early environment than *Manica* workers: their ability to learn was greater, leading them to care for more allospecific brood than *Manica* workers, who demonstrated a preference for conspecific brood, in all groups studied. These experiments also showed great variability in the expression of species polyethism among different groups of ants according to the degree of polygyny of the queen's species. The behavioural differences observed in *Manica* and *Myrmica* species might be due to the phyletic distance between the two genera.

KEY WORDS: ants, Myrmicinae, polyethism, mixed colonies.

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INTRODUCTION

Insect societies are essentially characterized by a division of labour among their members. This phenomenon, called polyethism (WEIR 1958a, 1958b), implies the formation of specialized groups within the society in which individuals perform the same activities.

The division of labour appears in the worker caste according to the ants morphology (e.g., the "soldiers" in some species of ants) and/or age (WILSON 1975, PASSERA 1984, HÖLLDOBLER & WILSON 1990).

In fact, we know that young workers tend to stay in the nest to care for the brood, even though, as they grow older, they can leave the nest for outside activities like foraging. Besides these two castes, some workers called "intermediate" (BRIAN 1974) or "domestic" (WEIR 1958a, 1958b) are somewhat polyvalent, being slightly, or not at all, specialized.

Nevertheless, this dynamic correlation, age/polyethism, is not strict. In fact, numerous studies have shown that individuals belonging to the same caste, possessing the same morphology and age, could have different functions in the society (BRIAN & BRIAN 1952, BLUM 1977, LENOIR 1979). This individual variability (idiosyncrasy) provides evidence for a behavioural plasticity which allows ants to adapt to changes occurring in their physical or social environment. This plasticity was demonstrated through experiments in which a given functional group is excluded from the society. After such an exclusion, a phenomenon of social regulation takes place: remaining individuals perform an activity that they would not normally perform in order to restore social stability (LENOIR 1979, LACHAUD & FRESNEAU 1987). This capacity for regulation is not surprising given the ability of both specialized individuals to change functions and generalist individuals to specialize in the functions needed by the social group.

Recently, several authors showed that the genetic components of the division of labour occur in at least three species of ants: *Leptothorax rudis* (STUART & PAGE 1991), *Formica argentea* (SNYDER 1992, 1993) and *Camponotus planatus* (CARLIN et al. 1993).

Polyethism was also studied by comparing queenless and queenright groups of ants. In *Cataglyphis cursor*, BERTON et al. (1992) observed a decrease in the activities of nursing and foraging in queenless groups. BRIAN & HIBBLE (1963) showed that in *Myrmica*, large larvae received more food from workers and are licked more often in queenright groups. However, these works dealt with only some behavioural items and not with all social activities.

Ant societies sometimes include two or more species, leading to the constitution of compound nests or mixed colonies (WASMANN 1891). In the former, two species live close to one another but the heterospecific broods are separated. These associations might, in fact, consist in only simple spatial proximity without direct communication between species (pleiobiosis is the most primary type of association in ants, see HÖLLDOBLER & WILSON 1990) or in true social parasitism (see HÖLLDOBLER & WILSON 1990). In mixed colonies, the heterospecific broods are reared together and these associations come from social parasitism (see reviews of PASSERA 1984, HÖLLDOBLER & WILSON 1990). These kinds of mixed colonies can be reproduced in the laboratory by associating adult ants (JAISSON 1980, CARLIN & HÖLLDOBLER 1983, ERRARD 1984, BAGNERES et al. 1991, CORBARA & ERRARD 1991) or through the adoption of brood (PLATEAUX 1960, 1985; VIENNE et al. 1992). This model of artificial mixed colonies was used to investigate the phenomena of early learning, behavioural plasticity and recognition. In these works, the authors studied some behavioural items but never investigated the entire division of labour.

In this context, by means of observations, we established the behavioural repertoire (ALTMAN 1965) of the sub-castes of workers (in our case, workers of both species associated in mixed groups, with or without a queen, were considered as sub-castes). In analyzing the social organization of heterospecific groups, we wanted to know if a division of labour existed among workers according to the species to which they belonged (species polyethism). On the other hand, we used queenless and queenright heterospecific groups to see if the queen is involved in the establishment of polyethism in ant societies.

MATERIALS AND METHODS

Species, constitution of experimental groups and housing conditions

Three species of Myrmicinae ants were collected in June 1989 and May 1991. *Manica rubida* which is an oligogynous species (two or more queens coexist in the same nest but remain separate from one another, HÖLDOBLER & WILSON 1990) was found in Morillon in the French Alps (700 m in altitude). *Myrmica ruginodis* (macrogyne form, monogynous species) colonies were collected near Tours, France. Colonies of *Myrmica rubra*, a species with a high degree of polygyny and which lives in plesiobiosis with *Manica rubida*, were collected in Morillon.

We created queenright and queenless heterospecific groups in which workers of *Manica rubida* were associated before emergence, with, respectively, one of the two species of *Myrmica* (Table 1). We also created homospecific control groups (five of each species) containing 20 workers (queenless groups) or 20 workers + 1 queen (queenright groups).

Individuals were placed in glass vials (L = 20 cm, 1.7 cm in diameter) with a water reservoir at one extremity and a cotton plug at the other, which was used to close the nest and through which food (mealworm larvae, flies and a honey/apple mixture) was introduced twice a week. We created obscurity in the vial with a piece of removable black cardboard. All the tubes were maintained under the same conditions: temperature of 22 ± 3 °C, humidity of 60% and photoperiod 8-20 hr.

Myrmicinae pupae are nude and can emerge alone. Coming from mature colonies, they thereby yielded normal-sized workers (WOOD & TSCHINKEL 1981) and not dwarf workers which have a different type of behaviour adapted to the foundation of a colony (PORTER &

Table 1.
Constitution of experimental heterospecific groups.

<i>M. rubida</i>	10 pupae	10 pupae	10 pupae + 1 queen	10 pupae	10 pupae + 1 queen	10 pupae
<i>M. rubra</i>	10 pupae		10 pupae	10 pupae + 1 queen		
<i>M. ruginodis</i>		10 pupae			10 pupae	10 pupae + 1 queen
Number of groups	5	5	5	5	5	5
	10 queenless heterospecific groups (association of pupae)		20 queenright heterospecific groups (adoption of pupae by a queen)			

TSCHINKEL 1986). Pupae given in adoption to queens could be their own, but not necessarily. This was impossible to assess especially for *Myrmica rubra*, which is a species with a high degree of polygyny. Every day, the newly-laid eggs of the queens were removed and we replaced all rejected or "injured" pupae. The five groups of the same type were constituted from the same mother colony. Queenless groups were formed in July 1989 and queenright ones in August 1991. All *Myrmica rubra* and *Myrmica ruginodis* queens, and two *Manica rubida* queens came from mother colonies collected in the field; we did not know their age. The other *Manica rubida* queens were foundresses, fertilized in the laboratory and isolated after they lost their wings.

Method

In order to establish the ethograms of individuals from the different groups, we used the automated photographic record technique perfected by CORBARA et al. (1986). Two months after the constitution of the groups, individuals were removed to a plaster nest which included six shallow chambers, permitting us to observe the ants from a horizontal plane. The nest was covered with a plate of black glass and was connected to an external area (a plastic box 11 cm in diameter) by a supple polyethylene tube. We placed ants (not individually marked) in the external area and we added five medium-sized larvae from each species (five *Manica rubida* and five *Myrmica*). After a 24 hr period which permitted the ants to retrieve brood and familiarize themselves with their new nest, we removed the plate of black glass and we began an automatic photographic record at the rate of one picture every 30 min (the period suggested by CORBARA et al. 1988) during 3 nights and 2 days. After this, the ants were returned to their original tube. We placed food in the external area during the first day of recording. We made black and white slides from the films, which we viewed under a binocular lens. This enabled us to assign one behavioural item to each individual. One hundred slides were analyzed per group in order to build the ethograms of individuals for each species. We could distinguish the larvae of the associated species by their size and shape which permitted us to compare the respective part of care given to these two types of brood. Only the nest was photographed. It was assumed that each ant not found on a slide was performing an outside activity.

Treatment of data: analysis of results

All the different behavioural items were grouped into 21 classes (Table 2). Behavioural items directed toward eggs appeared in this ethogram because queens laid eggs during the 3 days of observation. It was then impossible to remove the eggs without interfering with the behaviour of ants.

A software package perfected at the laboratory permitted us to obtain items (observed data) which we used as matrixes. We then applied, in a global manner, a discriminant analysis (CSS Package) to determine which variable (a combination of behavioural items) discriminated between two or more groups and to classify these variables according to their discriminant power (F) and its significance (P). The greater F, the greater the discriminant value of a variable. We used Mann Whitney and Wilcoxon tests in a more detailed analysis. Figures show the mean frequency of behavioural items with standard deviation (SD) and the results of Mann Whitney U test. The results of the Wilcoxon test are reported in the text. For interactions among adults, we noted the caste (queen or worker) and the species of the donor and the receiver. Values of given social interactions (GSI) and received social interactions (RSI) were not always equal. In fact, if an individual both received an interaction and displayed a behavioural item, we chose to record its action and not the received interaction because we could not assign two items per individual per slide.

Table 2.
General ethogram (alphabetical order).

Code	Behavioural items	Description of items
ABC	Allospecific brood care	Licking or feeding or grooming allosp. eggs or larvae, anal grooming to allosp. larvae, giving trophallaxis to allosp. larvae
ABT	Allospecific brood transport	Transport of allospecific eggs or larvae
CAL	Cannibalism on allospecific larvae	Eating an allospecific larva
CBC	Conspecific brood care	Licking or feeding or grooming consp. eggs or larvae, anal grooming to consp. larvae, giving trophallaxis to consp. larvae
CBT	Conspecific brood transport	Transport of conspecific eggs or larvae
CCL	Cannibalism on conspecific larvae	Eating a conspecific larva
CQ	Cares for the queen	Grooming or anal grooming or giving trophallaxis to the queen
DAN	Domestic activities in the nest	Digging or transporting plaster, antennal exploration or transport of different materials or rubbish
EAB	Antennal exploration of allospecific brood	Exploration with antennae of allospecific eggs or larvae
ECB	Antennal exploration of conspecific brood	Exploration with antennae of conspecific eggs or larvae
FAN	Food activities in the nest	Antennal exploration or eating or transporting a prey or liquid or glucid, cutting up a prey, eating proteins
GN	Guard in the nest	Guard at the entrance or in the nest
GSI	Given social interactions	Antennal contact with another worker, grooming or anal grooming a worker, giving trophallaxis to a worker, licking a worker, carrying a worker
IAB	Inactivity on the allospecific brood	Immobility with physical contact (non-antennal) on allospecific eggs or larvae
ICB	Inactivity on the conspecific brood	Immobility with physical contact (non-antennal) on conspecific eggs or larvae
IN	Inactivity in the nest	Immobility
INQ	Inactivity near the queen	Immobility close to the queen
NAN	Non-specific activities in the nest	Anal self-grooming, self-grooming, flexion of the gaster bending over the soil, going in or out of the nest, moving around, licking the soil or walls of the nest
OA	Outside activities	Ant not observed in the nest
OVP	Oviposition	Queen in laying position, queen with bent gaster
RSI	Received social interactions	Antennal contact received from a worker, received grooming or anal grooming, received trophallaxis, licked by a worker, carried by a worker

RESULTS

Global analysis

We compared the behaviour of *Manica rubida* workers to the behaviour of *Myrmica* workers (*Myrmica rubra* and *Myrmica ruginodis*) for all heterospecific groups (queenless and queenright, $n = 30$).

Nine behavioural items had a significant discriminant value between these two groups (Table 3). Four of them were activities toward brood (allo and conspecific) that *Myrmica* workers carried out more often. These latter guarded the nest more often than did *Manica* workers. In contrast, *Manica* workers received more social interactions, and performed more domestic and non-specific activities than did *Myrmica*. They also went outside the nest more frequently.

Detailed analysis (separate observations on each type of heterospecific group)

Queenless groups. We noted four significant differences between the behaviour of *Manica rubida* workers and *Myrmica rubra* workers (Fig. 1A). The latter guarded the nest and cared for allospecific brood (EAB and ABC) more often than *Manica rubida* workers; who left the nest more frequently. *Manica rubida* workers cared for conspecific more than for allospecific brood ($T = 0$, $P = 0.043$). In contrast, we saw no species-level polyethism between *Manica rubida* workers and *Myrmica ruginodis* workers reared together in queenless groups (Fig. 1B). However, *Manica rubida* workers preferred to care for conspecific rather than for allospecific brood ($T = 0$, $P = 0.043$). They also initiated more social interactions than they received ($T = 0$, $P = 0.043$).

Queenright groups. We observed many significant differences between *Manica rubida* and *Myrmica rubra* workers especially when reared with a *Manica rubida* queen (Fig. 2). In both cases (with a *Myrmica rubra* queen and with a *Manica rubida* queen), *Myrmica* workers guarded the nest, explored allospecific brood more frequently and received less social interactions than *Manica* workers. In groups containing a *Myrmica rubra* queen (Fig. 2A), they also transported conspecific brood more frequently than *Manica* workers. In this association, *Manica* workers performed more activities toward conspecific than toward allospecific brood ($T = 0$, $P = 0.043$ for inactivity on brood, brood transport and brood care). This was also the case for brood care by *Myrmica rubra* workers. With a *Manica* queen (Fig. 2B), *Manica* workers performed more domestic activities and non-specific activities in

Table 3.

Significant behavioural differences between *Manica* workers and *Myrmica* workers (*M. rubra* and *M. ruginodis*) in queenless and queenright heterospecific groups (discriminant analysis).

Behavioural items	F	P
Antennal exploration of conspecific brood	16.68	0.00015
Received social interactions	11.89	0.0011
Guard in the nest	10.54	0.002
Domestic activities	7.6	0.008
Non-specific activities in the nest	6.87	0.011
Allospecific brood care	6.73	0.012
Allospecific brood transport	6.12	0.016
Outside activities	5.75	0.02
Conspecific brood transport	4.85	0.032

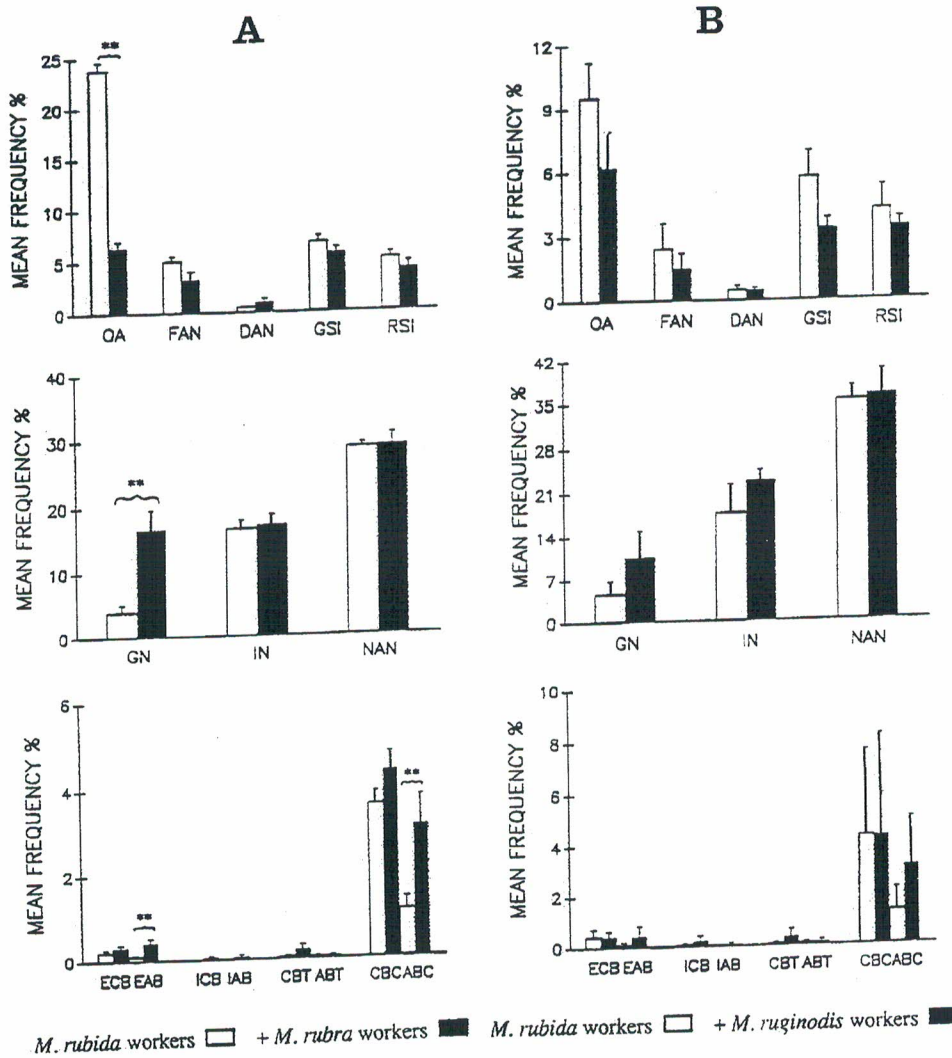


Fig. 1. — Ethogram of workers reared in queenless heterospecific groups (Mann Whitney U test: ** $P < 0.02$).

the nest, engaged in more cannibalism on allospecific larvae, and initiated more social interactions with workers of both species than *Myrmica rubra* workers. *Myrmica rubra* workers stayed more frequently near the queen and on allospecific brood (IAB) and cared more for allospecific brood than did *Manica* workers. We found also that *Manica* workers preferred to care for conspecific rather than allospecific brood ($T = 0, P = 0.043$). Workers of both species initiated more interactions than they received ($T = 0, P = 0.043$).

There was no polyethism among workers of either species in the association between *Manica* and *Myrmica ruginodis* when the queen of the group was from the

Manica species (Fig. 3A). However, *Manica* workers preferentially directed their activities toward conspecific rather than allospecific brood ($T = 0, P = 0.043$ for antennal exploration and care). This was the case for *Myrmica ruginodis* workers concerning brood transport ($T = 0, P = 0.043$). In contrast, we noted nine significant differences in the behaviour of workers of both species when reared together with a *Myrmica ruginodis* queen (Fig. 3B). *Manica* workers left the nest more frequently, initiated and received more interactions, performed more non-specific activ-

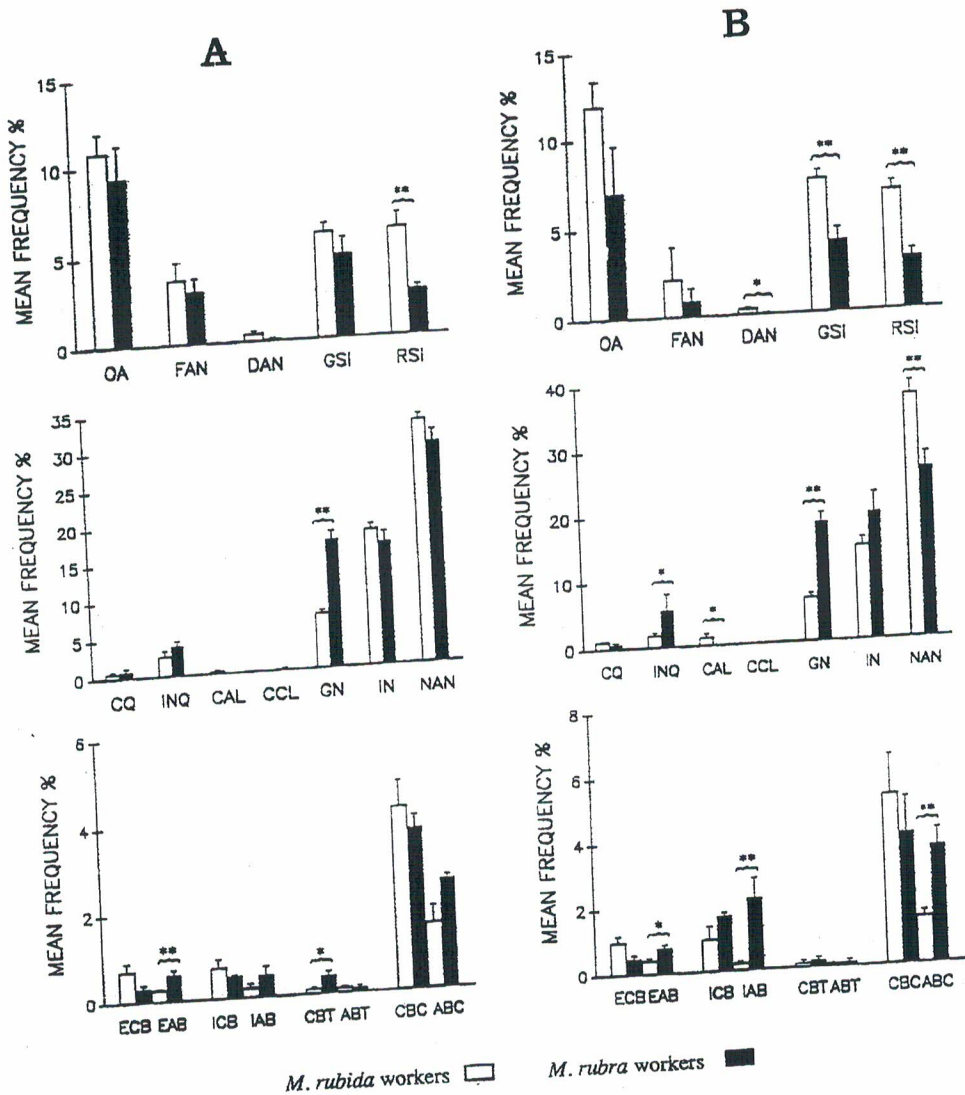


Fig. 2. — Ethogram of workers reared in queenright heterospecific groups with a *Myrmica rubra* queen (A) and with a *Manica rubida* queen (B) (Mann Whitney U test: ** $P < 0.02$, * $P < 0.05$).

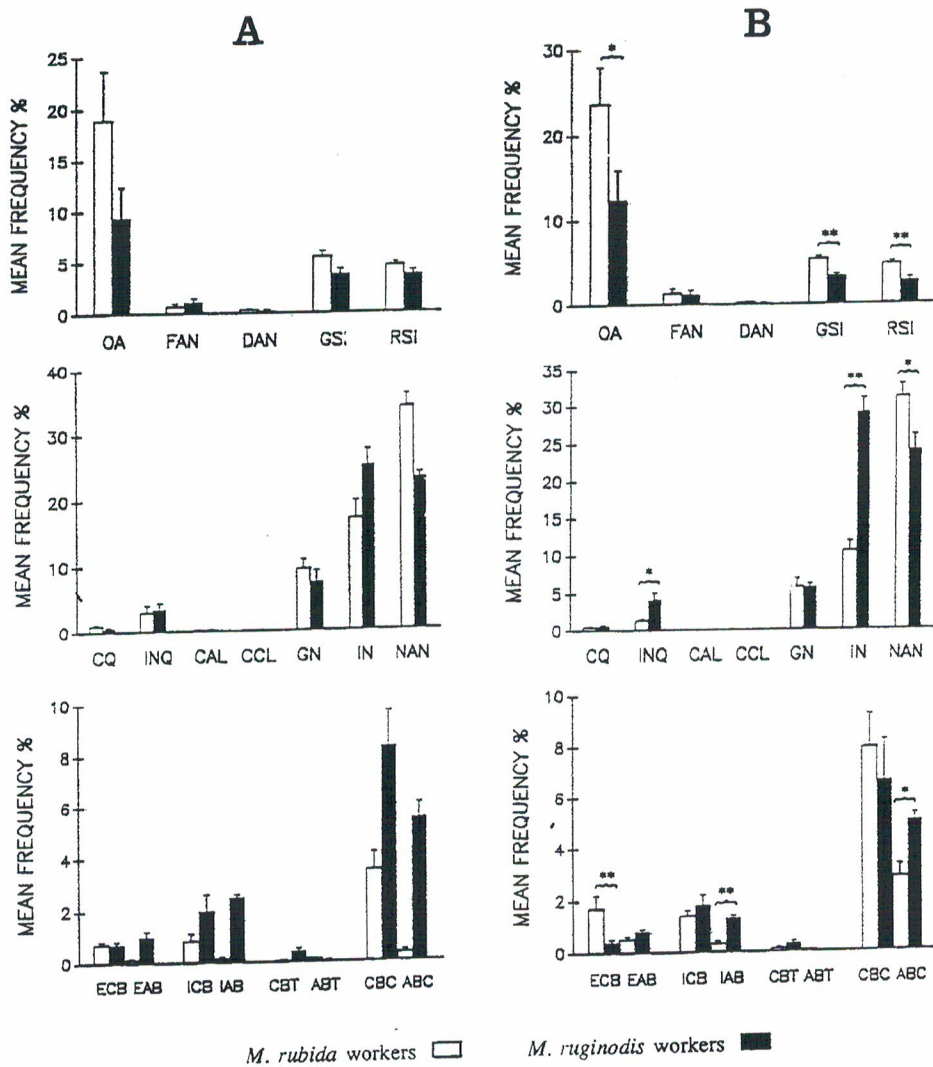


Fig. 3. — Ethogram of workers reared in queenright heterospecific groups with a *Manica rubida* queen (A) and with a *Myrmica ruginodis* queen (B) (Mann Whitney U test: ** $P < 0.02$, * $P < 0.05$).

ities in the nest and explored conspecific brood with antennae more than *Myrmica ruginodis* workers. The latter seemed to be more inactive in the nest (IN), remaining near the queen (INQ) and on allospecific brood (IAB) more often than did *Manica* workers. They also displayed more allospecific brood care. *Manica* workers showed a preference for conspecific rather than for allospecific brood ($T = 0$, $P = 0.043$ for antennal exploration, inactivity on brood and brood care). *Myrmica ruginodis* workers displayed this trait only for brood transport ($T = 0$, $P = 0.043$).

DISCUSSION

Our results indicate that these associations are more than simple cohabitation, since we observed interspecific altruism (brood care, mutual grooming and trophallaxis) and no agonistic interactions between individuals from the two species. This is quite different from the results obtained by CORBARA & ERRARD (1991) concerning heterospecific groups of two species belonging to different sub-families, *Formica selysi* (Formicinae) and *Manica rubida* (Myrmicinae) wherein each keeps its species-specific spatial and social characteristics. In our case, we have a true fusion of associated species that leads to the constitution of completely-integrated societies. The high level of integration between workers of both species is apparent in the percentage of eaten larvae which dropped from 78% in homospecific control groups to 14% in heterospecific groups. This point confirms the probability that success in creating heterospecific colonies increases when more closely related species are used (JAISSON 1980, ERRARD 1984). *Manica rubida* and the two *Myrmica* species are phylogenetically close, both belonging to the subfamily of Myrmicinae and they were for a long time classified in the same genus.

We may note, however, that a polyethism corresponding to species specialization was observable, despite the fact that the individuals were of the same age and that the species were phylogenetically close. This phenomenon has already been reported for many species of ants such as *Lasius niger* (LENOIR 1979), *Novomessor albisetosus* (MCDONALD & TOPOFF 1985), *Solenopsis invicta* (SORENSEN et al. 1985), *Camponotus abdominalis* (ERRARD 1985) and *Ectatomma ruidum* (B. CORBARA in preparation), and for the honey bee *Apis mellifera* (WINSTON & FERGUSON 1984). It has also been reported in queenless mixed groups of *Camponotus senex*/*C. abdominalis*, *C. senex*/*Pseudomyrmex ferruginea* (ERRARD 1984).

In our associations, *Myrmica* workers specialized in brood care and guarding of the nest (both activities in the nest) while *Manica* workers performed activities normally reserved for the oldest workers (domestic activities, activities outside the nest and activities requiring mobility).

We can not explain this result by species polymorphism between workers. If polymorphism was implied, the behavioural differences between *Manica* and *Myrmica* would be the same in the different associations, because *Myrmica rubra* workers and *Myrmica ruginodis* workers are the same size.

So we assume that there is an effective species polyethism in these mixed groups. However, this species polyethism might have been induced by age differences in workers of the species reared together despite the fact that we used pupae of the same age for the constitution of the heterospecific groups. In fact, this virtual age should be defined in terms of longevity of each species which might be different because of their different degrees of polygyny. In this case, two months do not represent the same age on the respective life duration scales of the species and this might be sufficient to create behavioural differences.

Another possible explanation for this species polyethism is that ethogenesis (the development of behaviour) in *Manica rubida* workers is more rapid and therefore they carry out some activities which are usually characteristic of the oldest workers, earlier in their lives than *Myrmica* workers. This point was confirmed by observations on homospecific control colonies in which *Manica* workers left the nest more frequently than do *Myrmica rubra* and *Myrmica ruginodis* workers though they were the same age (VIENNE 1993). Therefore, the species polyethism in our groups might be explained by this difference in the ethogenesis of individuals. The very

early maturation of *Manica rubida* workers is also observable in their physiology: their chemical signature develops very soon after emergence (HEFETZ et al. 1992).

However, species polyethism is not the same in the different associations of species described here. In fact, in queenless groups, species polyethism is null in the association *Manica rubida*/*Myrmica ruginodis* highly developed in the association *Manica rubida*/*Myrmica rubra* (four significant differences). In queenright groups, we observed four significant differences between the behaviour of *Manica rubida* and *Myrmica rubra* workers when reared with a *Myrmica rubra* queen and 10 when reared with a *Manica rubida* queen. We saw no significant difference (no polyethism) in groups associating *Manica rubida* workers and queen to *Myrmica ruginodis* workers, but nine significant differences when the queen is from the *Myrmica ruginodis* species. These results show that there is great individual variability in the behaviour of ants, something which has been increasingly demonstrated over the last few years (see HÖLDOBLER & WILSON 1990).

Polyethism seems greater in queenright than in queenless groups. Therefore, the queen appears to be an organizational factor for the society: her presence structures worker activity.

For the association *Myrmica rubra*/*Manica rubida*, the degree of polyethism is greater when the queen is from the *Manica rubida* species, and for the association *Manica rubida*/*Myrmica ruginodis* polyethism is greater when the queen is from the *Myrmica ruginodis* species. The important factor is certainly the degree of polygyny of the species. We know that in a monogynous species, the queen has a greater influence on workers than in a polygynous species. She is bigger, with more developed ovaries and lays more eggs: therefore, workers are more attracted to her than in polygynous societies where queens do not have the same fecundity and have a variable and lower power of attraction over workers (CAMMAERTS 1985; CARLIN & HÖLDOBLER 1986, 1987; KELLER 1988). The influence of the queen being more obvious, the group might be more organized in terms of division of labour. So, when we associate a monogynous and an oligogyne species, polyethism is greater in groups with a queen from the monogynous species. When we associate a polygynous and an oligogyne species, the polyethism is greater in groups with the queen from the oligogyne species.

It was also shown that, in heterospecific groups, *Myrmica* workers cared more for allospecific brood than *Manica* workers. They cared for both species of brood at the same frequency, in contrast to *Manica* workers who preferred conspecific brood.

We cannot explain this point by the fact that polygynous species are known to be more tolerant of foreign individuals than monogynous species (JANZEN 1973, HÖLDOBLER & WILSON 1977, DE VROEY 1979, LE ROUX 1980, CERDAN & PROVOST 1990, MOREL et al. 1990). *Myrmica rubra* is polygynous and *Myrmica ruginodis* is monogynous and both took care of allospecific as well as conspecific brood.

Therefore, individuals of the genus *Myrmica* seem to be more easily influenced by their early social environment than *Manica* individuals. In contrast, in *Manica*, the genetic factors determining recognition in adults are more important than environmental factors encountered just after emergence. *Myrmica* workers recognize as nestmates all individuals or larvae living in their nest during their early life (the principle of absolute confidence, see JAISSE 1993) while *Manica* workers preserve their species-specific recognition. We verified this point with encounters between conspecific and allospecific individuals to test aggressive behaviour (VIENNE 1993). In *Myrmica*, early learning seems to take the place of

genetically-determined recognition (see template). Therefore, workers of this genus do not discriminate between allo- and conspecific brood since they are more plastic in their behaviour than *Manica* workers. The species *Manica rubida* appears more rigid, with lesser ability for early learning, leading it to discriminate both types of brood. However, it is also possible that the preference of *Manica* workers for conspecific brood may be due to a greater capacity for an increased response to optimal stimuli (i.e. pupae of the right size).

In conclusion, species polyethism was observed in our heterospecific groups due to ethogenesis, which developed more rapidly in the *Manica* genus than in the *Myrmica* genus. Nevertheless, this kind of polyethism is subject to great variability in individual behaviour due to the influence of the queen. We might also mention that the phyletic difference between the two ant genera appears in the behaviour of these two types of individuals. We saw no relationship between the differences in individual behaviour according to their species and the degree of polygyny of the species to which they belong. The phyletic aspect is more important here. However, it appears that the influence of the queen on polyethism depends on the degree of polygyny of the species: queens from monogynous species seem to be more involved in the social structuring of the group.

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