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Influence of the Queen on Worker Behaviour and Queen Recognition Behaviour in Ants

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Abstract

We investigated the influence of the queen on worker behaviour in ants and their queen recognition behaviour. Queenless and queenright homo- and hetero-specific groups were created using three Myrmicinae species (*Manica rubida*, *Myrmica rubra* and *Myrmica ruginodis*). In homospecific groups, the presence of a queen contributed to an increase in the brood care, which had an effect on all other tasks of the group. In heterospecific groups, the presence of a queen led workers to care more for the conspecific brood. The queen appears to be a factor in the maintenance of both behavioural characteristics of the workers and the organization of the colony. The absence of the queen revealed some behavioural differences between species compared and populations that did not occur in queenright groups. Attractiveness tests were also conducted on these colonies. In homospecific queenright groups, workers were attracted both by unfamiliar conspecific and allospecific queens, but they were attracted more by the former. Therefore, queens appear to emit volatile pheromones which have a non-species-specific and a species-specific attractant effect. In heterospecific groups, workers were attracted more by an unfamiliar queen of the familiar species (even if allospecific) than by an unfamiliar conspecific queen, suggesting the importance of early social experience for the discrimination behaviour of adults.

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Introduction

In ant societies, the queen has a special status. She is, in most species, the only one to reproduce and she only performs activities tied to reproduction. She is groomed and fed by workers who care for her offspring. The queen is attractive to workers, leading them in many cases to form a retinue and move with her when she moves (Stumper 1956; Glancey et al. 1982; Cammaerts 1985; Glancey 1986; Berton et al. 1991; Cariou-Etienne & Passera 1993). This phenomenon of aggregation is based on the emission of pheromones by the queen. These attractive substances are, in general, different from recognition substances and have not been

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characterized as they have in bees (Hölldobler & Wilson 1990; Bourke & Franks 1995).

The queen has been shown to be the principal source of the colony odour in species such as *Camponotus* (Hölldobler 1962; Carlin & Hölldobler 1983, 1986, 1987), *Leptothorax lichtensteini* (Provost 1987) and *Linepitheme humile* (Keller & Passera 1989). However, she appears to have a secondary role, or none at all, in *Pseudomyrmex ferruginea* (Mintzer 1982), *Leptothorax ambiguus* (Stuart 1985, 1988), *Solenopsis invicta* (Obin & Vander Meer 1988, 1989), *Rhytidoponera confusa* (Crosland 1990), *Cataglyphis niger* (Soroker et al. 1996) and *Cataglyphis cursor* (Berton et al. 1991). Only a few chemical analyses were conducted on the role of the queen in colonial odour. In *Formica* sp., Yamaoka (1990) showed that queenless workers lost their chemical colonial homogeneous identity after 10 days. This identity was recovered as soon as the queen was reintroduced into the queenless group. In *C. niger*, Soroker et al. (1996) showed that the queen did not contribute to the colony odour, which was confirmed in *Cataglyphis iberica* by Dahbi & Lenoir (in press).

In *C. cursor*, Berton et al. (1992) observed a decrease in worker activities of nursing and foraging in queenless groups compared with queenright groups. In queenright colonies of the *Myrmica* genus, Brian & Hibble (1963) showed that large larvae receive more food from workers and are licked more often than in queenless colonies. They also observed that in such colonies, these larvae are more often bitten by workers than in queenless colonies, an action that may reduce their growth and lead to the production of fewer new queens. Therefore, the queen contributes directly to the regulation of the number of workers and of reproductive females in her colony, as was also demonstrated by Ross (1988) in *Solenopsis invicta*. The queen reduces dominance exchanges and aggression between workers of the same colony and inhibits the ovarian development of workers through the use of pheromones (Hölldobler & Wilson 1990). We have shown that species-typical polyethism patterns are more obvious in queenright than in queenless heterospecific groups of ants, especially when the queen is from a monogynous species (Vienne et al. 1995).

Vienne (1993) recently suggested that the presence of a queen within a group could have an influence on workers' sensitivity to pheromones and/or on their learning ability. This first point supports previous results obtained by Jaisson (1972) from *Formica polyctena*, which demonstrated that the imprinting of young workers by simple association with cocoons is facilitated by the presence of the queen.

The aim of our study was to investigate the influence of the queen on worker behaviour and on social organization. We hypothesized that quantitative changes in the frequencies of behaviours would appear between queenless and queenright groups. We used homo- and hetero-specific groups of ants to see if this influence occurred in the same way in these two types of rearing schemes and especially if the species of the queen is important to worker behaviour. We also evaluated the queen recognition behaviour of workers reared in homo- or hetero-specific queenright groups toward unfamiliar allospecific and conspecific queens.

Materials and Methods

Species, Constitution of Experimental Groups, and Housing Conditions

Three species of Myrmicinae ants were collected in France, in Jun. 1989 and May 1991. *Manica rubida* came from Morillon in the Alps (altitude 700 m above sea level). *Myrmica ruginodis* (macrogyne form) colonies were collected near Tours. *Myrmica rubra* came from Morillon where it can be found in plesiobiosis (intimate cohabitation of different species of ants in the same nest but in different chambers, without any direct communication between heterospecific individuals; Hölldobler & Wilson 1990) with *Manica*. We used another population of *Myrmica rubra* originating from Tours to investigate some possible behavioural differences between the two populations. *Manica* do not live in the area of Tours.

We created 15 queenless heterospecific groups in which 10 worker pupae of *Manica* were associated with, respectively, 10 worker pupae of one of the two species and populations of *Myrmica* (five groups for each type of association). Thirty queenright heterospecific groups were constituted through the adoption of worker pupae (10 per species or population) by a single queen (10 groups for each type of association: five with a *Manica* queen and five with a *Myrmica* queen). We also created homospecific control groups (five of each species or population) containing 20 workers (20 queenless groups) or 20 workers plus one queen (20 queenright groups). A total of 80 colonies was created.

Individuals were placed in glass vials (20 cm long, 1.7 cm diameter) with a water reservoir at one end 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 per week. We darkened the vial with a piece of removable black cardboard. All the vials were maintained under the same conditions: temperature of 22 ± 3°C, humidity of 60% and photoperiod 12/12 h light/dark cycle.

Pupae are naked in Myrmicinae 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 & Tschinkel 1986). Pupae given in adoption to queens could be theirs, but not necessarily, because it was impossible to say, especially for *M. rubra* (which is a species with a high degree of polygyny) if the pupae given in adoption to queens are theirs or not. The five groups of the same type were constituted from the same mother colony. Queenless groups were formed in Jul. 1989 and the queenright ones in Aug. 1991.

All *M. rubra* and *M. ruginodis* queens, and 2 *Manica* queens came from mother colonies collected in the field: we did not know their age. The other *Manica* queens were foundresses, naturally fertilized (by males) in the laboratory and isolated after losing their wings.

Behavioural Assay

In order to establish the ethograms of individuals from the different groups, we used an automated photographic record technique developed by Corbara et al. (1986).

Two months after the establishment of the groups, individuals were moved 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 (an 11 cm diameter plastic box) by a supple polyethylene tube. We placed ants (not individually marked) in the external area and added five medium-sized larvae from each species (five *Manica* and five *Myrmica*).

After a 24-h period, which permitted the ants to retrieve brood and familiarize themselves with their new nest, we removed the black glass plate and we began an automatic photographic record at the rate of one picture every 30 min. (period determined by Corbara et al. 1988) for three 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 data-gathering.

We made slides from the films, which were viewed under a binocular lens. This enabled us to assign one behaviour to each individual. One-hundred slides were analysed 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 amount of care given to these two types of brood. Only the nest was photographed. It was supposed that each ant not found on a slide was outside.

All the different behavioural items were grouped into the following classes: allospecific or conspecific brood care (licking, feeding or grooming eggs or larvae), allospecific or conspecific brood transport (transport of eggs or larvae), cannibalism on allospecific or conspecific larvae (eating a larva), care of the queen (grooming or providing trophallaxis to the queen), domestic activities in the nest (digging or transporting plaster, antennal exploration or transport of different materials or rubbish), antennal exploration of allospecific or conspecific brood (exploration with antennae of eggs or larvae), activities related to food in the nest (antennal exploration or eating or transporting a prey or liquid or glucide, cutting up a prey, eating proteins), guarding of the nest, social interactions (given and received antennal contact, grooming, trophallaxis, mutual carrying), inactivity on the allospecific or conspecific brood, inactivity in the nest, inactivity near the queen, nonspecific activities in the nest (self-grooming, flexion of the gaster, exploration in the nest), outside activities, oviposition.

Behavioural items directed toward eggs appeared in this ethogram because queens laid eggs during the 3 d of observation. It was then impossible to remove the eggs without interfering with the behaviour of the ants, so these were left and taken into account. A software package developed in the laboratory permitted us to obtain matrices of items (observed data). The comparison of behavioural items and frequencies of ants from colonies (or groups) with different social rearing conditions was performed by a discriminant analysis.

Queen Attractiveness Tests

In order to test the queen recognition behaviour by workers, we used the experimental device presented in Fig. 1. For each group, five workers of each

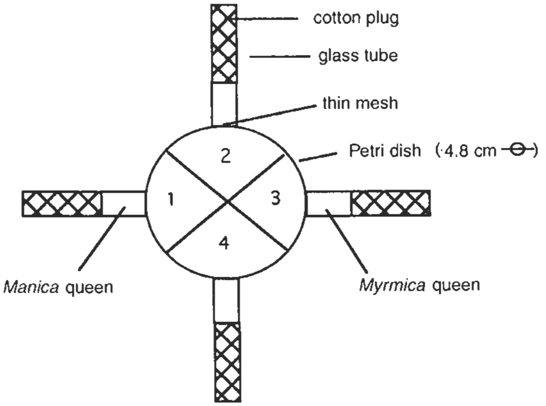


Fig. 1: Experimental device used to evaluate the queen recognition behaviour of workers

species or 10 for homospecific groups, were introduced simultaneously into the Petri dish which was closed with a cover labelled with the numbers of areas of the system (from one to four). Every minute over 30 min, we recorded the number and the species of ants found in each area.

Workers from the heterospecific groups were tested with two unfamiliar queen's of the species composing the groups: one *Manica* (area 1) and one *Myrmica* (area 3). *Myrmica* workers from control groups were tested with a *Manica* queen (area 1) and an unfamiliar conspecific queen (area 3). *Manica* workers from control groups were tested with an unfamiliar conspecific queen (area 1) associated, consecutively, with a queen from the two species and populations of *Myrmica* (area 3). The system was under neon-lighting to avoid any bias caused by phototropism and washed before each test with alcohol and dried.

For each area and for each of the 30 records, the number of ants from the same species over the five groups of the same type were totalled. The number of ants in the different areas were compared using the sign test (Siegel 1956).

Results

Worker Behaviour

Comparisons between queenless and queenright groups

We evaluated the influence of the queen on worker behaviour by comparing all queenless colonies (homo- and hetero-specific) to all queenright colonies, for all species, together with discriminant analysis. Behavioural items of the 80 colonies from the four experimental conditions were analysed (Fig. 2). A plot of the first and the second variables shows that colonies clustered in three separate groups. The first discriminant variable separated queenless colonies (blank spots) from queenright colonies (black spots). Within the queenright group, clusters appeared according to social rearing conditions: homo- and hetero-specific colonies were

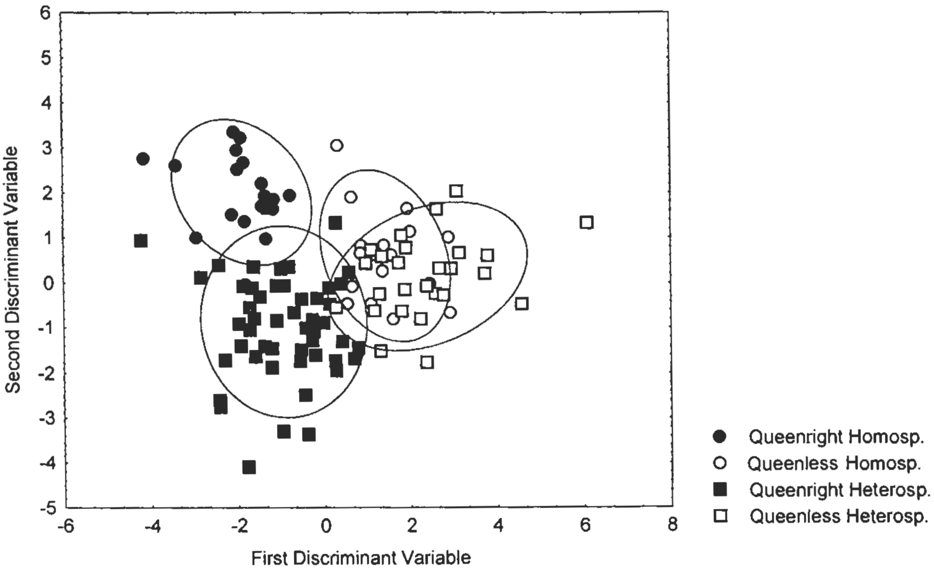


Fig. 2: A plot of the first two principal variables in the discriminant analysis of behaviour items of the four rearing social conditions (queenright and queenless homo- and heterospecific colonies). Each colony group is surrounded by the confidence ellipse ($p < 0.05$)

well separated by the second discriminant variable. The behavioural items dividing these groups were, for the most part, activities directed toward brood. In queenright colonies, the queen led workers to pay more attention to allospecific and conspecific brood than in queenless colonies: workers explored them more often with antennae, stayed in contact with them and cared for them more. Therefore, the presence of a queen led workers to care more intensively for the offspring and to remain closer to them. Workers reared without a queen left the nest more frequently, guarded the nest more often, performed more activities related to food and gave more social interactions. Reared in homospecific queenright colonies, workers performed more domestic activities in the nest than workers reared in heterospecific queenright colonies.

The 44 queenless and queenright heterospecific colonies were analysed for all species together to evaluate the influence of the queen's species on the behaviours of the workers (allo- or conspecific queen) (Fig. 3). A plot of the first and the second variables shows that colonies clustered together, again forming three separate groups. The first discriminant variable separates queenless colonies from queenright colonies. Within the queenright groups, colonies grouping according to the nature of the queen is apparent, and colonies with a conspecific queen were separated from the colonies with an allospecific queen by the second discriminant variable. In queenless colonies, the analyses confirmed previous results (see

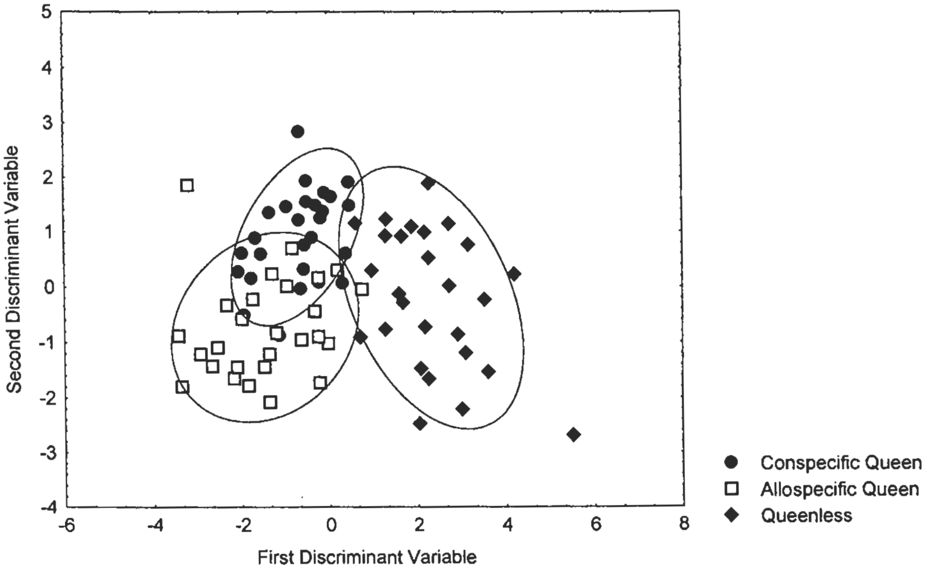


Fig. 3: A plot of the first two principal variables in the discriminant analysis of behaviour items of the three rearing social conditions (queenright with allospecific or conspecific queen and queenless heterospecific colonies). Each colony group is surrounded by the confidence ellipse ($p < 0.05$)

Fig. 1) — workers performed more domestic activities, less external activities and less allospecific and conspecific brood care. The comparison between workers reared with a conspecific queen and those reared with an allospecific queen showed that workers reared with the latter showed more (allospecific and conspecific) brood care (antennal contact and inactivity on the brood) than workers reared with the former. These latter gave more social interactions and performed more nonspecific activities.

Comparison between genera, species and populations

a. Genera and species comparisons. All the 80 homo- and hetero-specific colonies were analysed, comparing the species (Fig. 4): the ants clustered together forming three distinct groups according to the species. The first discriminant variable separates *Myrmica* colonies from *Manica* colonies. Within the *Myrmica* groups, colonies grouping according to the species of the ants are apparent, and *M. rubra* were separated from *M. ruginodis* ants by the second discriminant variable. The behaviours that had an important significant weight in the analysis were social interactions and external activity. *Manica* workers left the nest more often than *Myrmica* workers. This result confirms previous observations that *Manica* workers have a more rapid ethogenesis than *Myrmica* workers (Vienne et al. 1995).

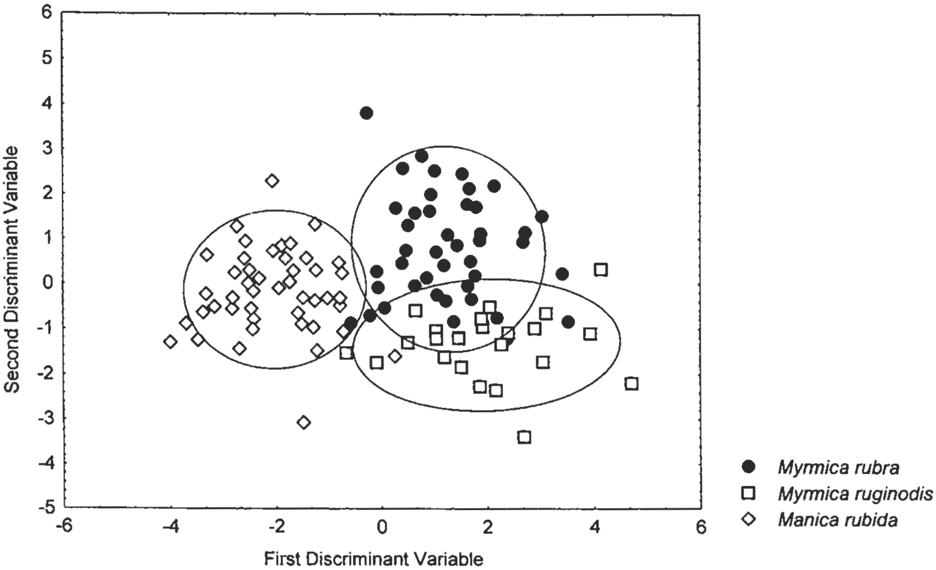


Fig. 4: A plot of the first two principal variables in the discriminant analysis of behaviour items of the three species reared in homo- and hetero-specific colonies (*Myrmica rubra*, *M. ruginodis*, *Manica rubida*). Each colony group is surrounded by the confidence ellipse ($p < 0.05$)

In this context, *Manica* workers performed less (allospecific and conspecific) brood care and less inactivity in the nest. *Myrmica* had more social interactions and performed more guarding of the nest than the other two species. *M. ruginodis* presented more inactivity in the nest than *M. rubra* and performed fewer nonspecific activities.

In a complementary analysis we observed, in queenright groups, differences in domestic activities (more often practised by *Manica* workers) and in care of the queen (more often for *Myrmica* workers). Therefore, significant differences between *Manica* and *Myrmica* workers were more numerous in queenright groups. The presence of a queen appeared to lead workers to behave according to the characteristics of the genus.

b. Species and populations comparisons in homospecific colonies. Behavioural items of the 26 colonies of different *Myrmica* species colonies (*M. rubra* and *M. ruginodis*) and different *M. rubra* populations colonies (Tours and Morillon) were analysed in queenless and queenright colonies (Fig. 5). A plot of the first and the second variables shows that ants clustered together forming three distinct groups when colonies were queenright (black spots) and three other well-separated groups when colonies were queenless (blank spots). The first discriminant variable sep-

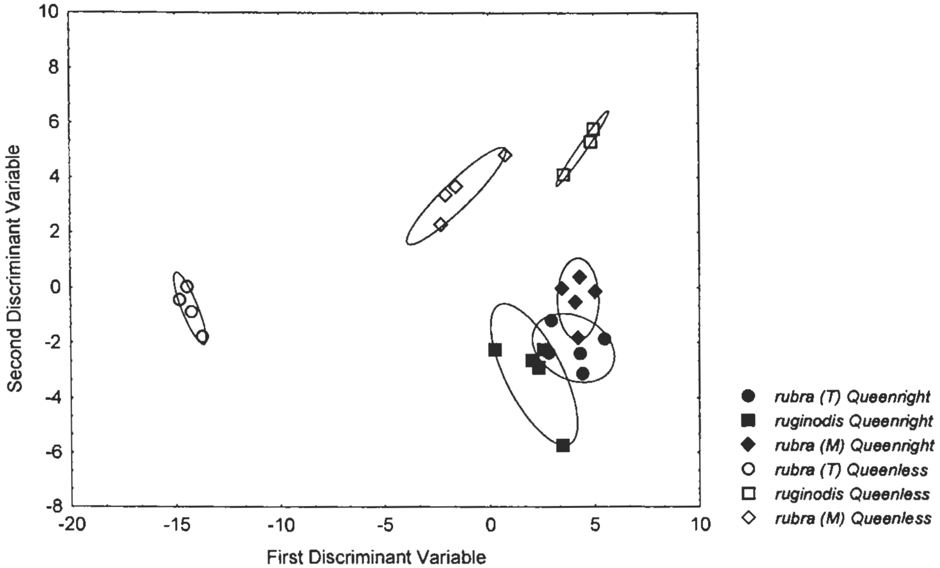


Fig. 5: A plot of the first two principal variables in the discriminant analysis of behaviour items of different populations of *Myrmica rubra* (Tours or Morillon) and *M. ruginodis* workers reared in queenright or queenless homospecific colonies. Each colony group is surrounded by the confidence ellipse ($p < 0.05$). T, Tours population; M, Morillon population

arates queenright *M. rubra* species colonies (Tours and Morillon populations) from queenright *M. ruginodis* species colonies, and separates the three queenless colonies as a function of the species and populations. Colony grouping according to the presence of the queen is apparent, and queenless *Myrmica* colonies were separated from queenright *Myrmica* colonies by the second discriminant variable.

In the comparison of the behaviour of workers within the genus *Myrmica*, six items were significantly different: given social interactions, inactivity in the nest, conspecific brood care, guarding the nest, nonspecific, food and external activities.

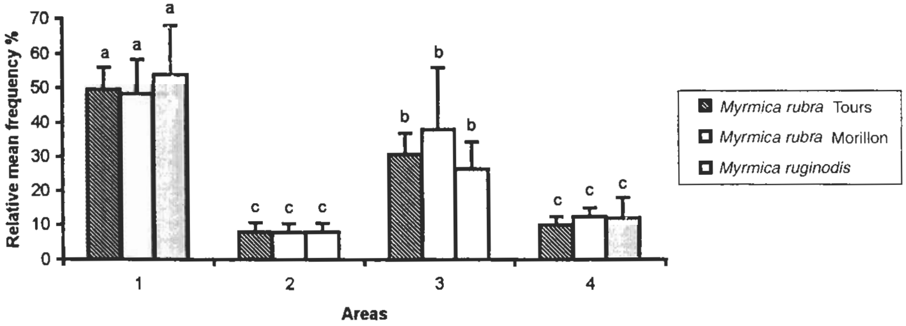
When we compared *Myrmica* species (*M. rubra* vs. *M. ruginodis*), the analyses showed that *M. ruginodis* performed less domestic and nonspecific activities than *M. rubra*. However, within queenless colonies, *M. ruginodis* performed more guarding of the nest and had less inactivity in the nest than *M. rubra*. This phenomenon recurred when we compared the two populations of *M. rubra* (Tours and Morillon). In fact, we observed eight significant differences in queenless groups: external and food activities, allospecific and conspecific brood care (antennal contact, inactivity on brood and brood care), but only two significant differences in queenright colonies (external activity and brood care).

Attractiveness Tests

Control groups

When reared in homospecific control groups, workers of all species exhibited a preference for the conspecific queen (39.8% vs. 30.4% for *M. rubra*, Tours, $z = 3.47$, $p < 0.001$; 52.7% vs. 23.7% for *M. rubra*, Morillon, $z = 5.3$, $p < 0.0001$; 39.5% vs. 29.6% for *M. ruginodis*, $z = 4.83$, $p < 0.0001$; and a mean of 48.3% vs. 31.7% for *Manica*, $z = 4.94$, $p < 0.0001$ for the three cases) (Fig. 6). This point reveals the existence of a species-specific attractive queen pheromone.

However, the allospecific queen also attracted workers, less often than the conspecific one, but more often than the neutral areas (Fig. 6) ($p < 0.00006$ for all the comparisons, except for *M. rubra* Tours workers from control groups when we compared area 1 and area 4, where $p = 0.027$). All the queens therefore seem attractive to workers, indicating that the queens may emit a caste nonspecific signal.


Manica rubida workers from control groups

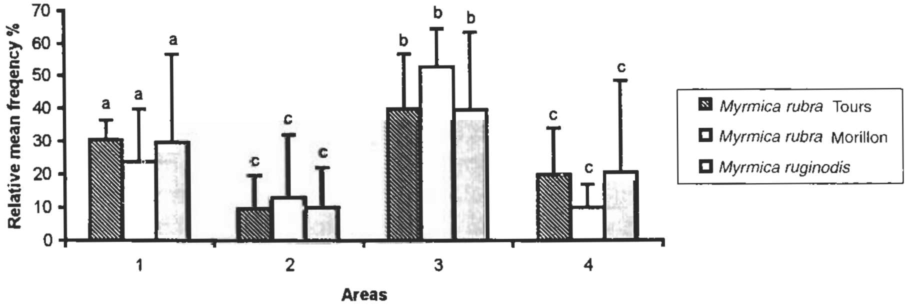

Myrmica workers from control groups

Fig. 6: Distribution of workers from homospecific control groups in the device used to evaluate their queen recognition behaviour (1, *Manica* queen area; 3, *Myrmica* queen area; 2 and 4, neutral areas). Different letters represent the groups which differed significantly

Heterospecific groups

To simplify the data we did not represent the neutral areas which are always unattractive to the workers. Reared in heterospecific groups, workers of both species in most of the cases tended to aggregate preferentially near the queen of the familiar species (queen of the species with which they were reared) even if allospecific: *Manica* when reared with a *Manica* queen and *M. rubra* when reared with a *M. rubra* queen except for *M. ruginodis* workers reared with a conspecific queen which exhibit a preference for the *Manica* queen (Figs 7, 8). The preference for the conspecific queen disappeared as a consequence of the neo-imaginal experience. However, this phenomenon was less obvious in *Manica* workers. The difference in aggregation around the two queens tested was not significant, although the frequency was slightly higher for the *Myrmica* queens, when they were reared with both workers and queens from *M. rubrai* Tours, and *M. ruginodis*.

Discussion

Our results showed that the presence of a queen within a group of ants had a great influence on worker behaviour. She stimulated contacts (active or passive) between workers and brood, and especially enhanced brood care. She appears to have an important role in social cohesion. This point can be compared with the results of Berton et al. (1991, 1992) in *Cataglyphis cursor* and Brian & Hibble (1963) in *Myrmica*, as well as those of Glancey et al. (1982) and Glancey (1986) in *Solenopsis invicta*.

In homospecific control groups, the presence of a queen led to an increase in brood care behaviour and a general decrease in all other activities. This is apparently different from the results of Berton et al. (1992) who observed a decrease in foraging activities in queenless groups, but it was just before hibernation and without brood. In our case, without a queen, activities normally reserved for the oldest workers (guarding of the nest, outside activities, food activities) were greater than in queenright groups although ants of these two kinds of groups were the same age. However, Berton et al. (1992) also observed a greater number of workers outside the nest, indicating a decrease in social cohesion.

We have noted that behavioural differences between *Myrmica* species and populations disappeared or became less numerous in queenright groups, whereas the converse occurred between the genera *Manica* and *Myrmica*. The presence of a queen could be the guarantor of the behavioural characteristics of an ant genus. Activities of the colony are organized around the queen and the brood (both are linked). Without a queen, the organization of the society is disturbed and differences between populations and species therefore become apparent, as was the case with our two populations of *M. rubra*. Results in queenless groups from these two populations could lead us to hypothesize that they are different species. However, the fact that no difference appears between them in queenright groups does not support this hypothesis. Nevertheless, on a behavioural point of view the two *Myrmica* species are closer than *Manica* species, indicating that behaviour could be a good index of phylogeny.

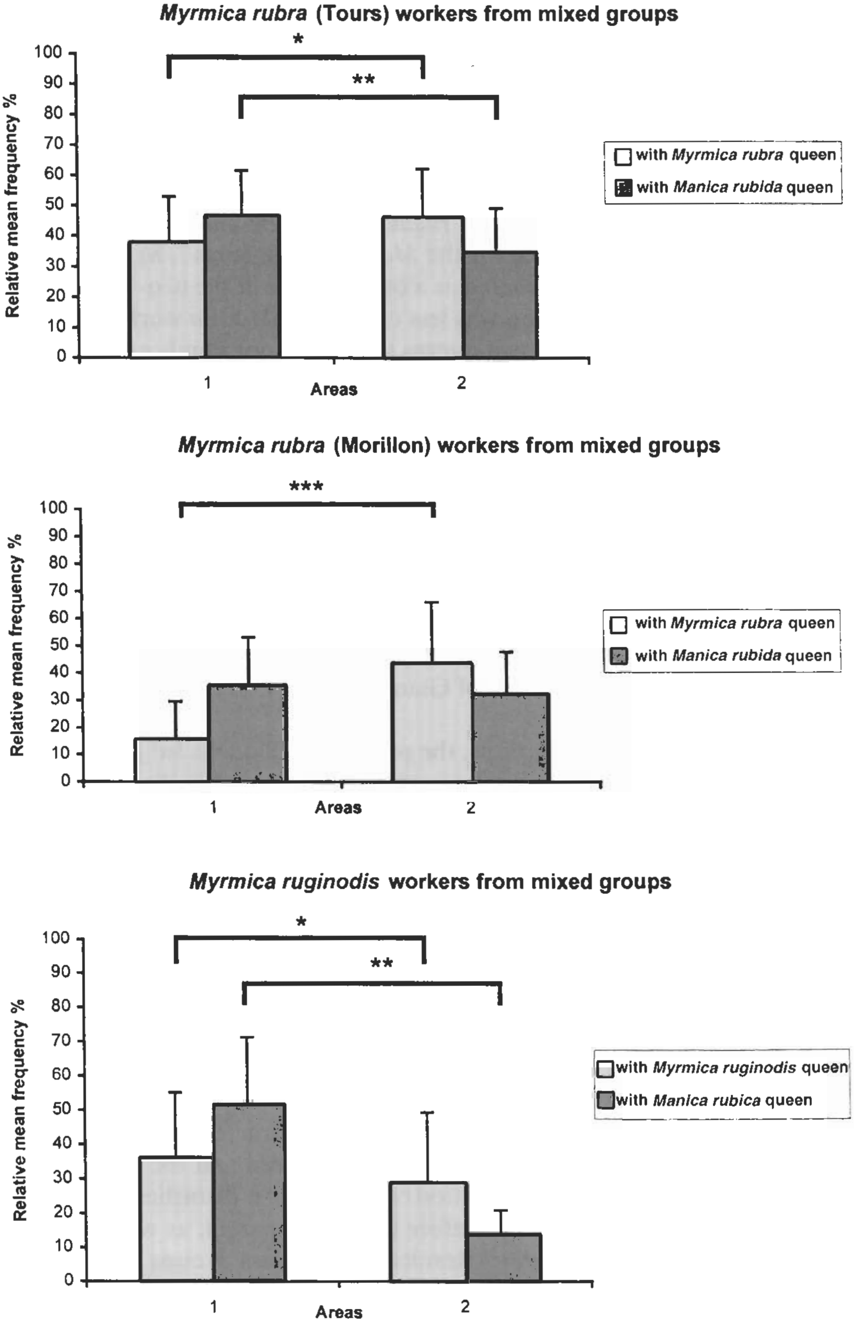


Fig. 7: Choice of aggregation of *Myrmica* workers reared in heterospecific groups around an allo- and conspecific queen (1, *Manica* queen area; 2, *Myrmica* queen area). $* p < 0.01$, $** p < 0.001$, $*** p < 0.0001$ (sign test). Neutral areas are not represented

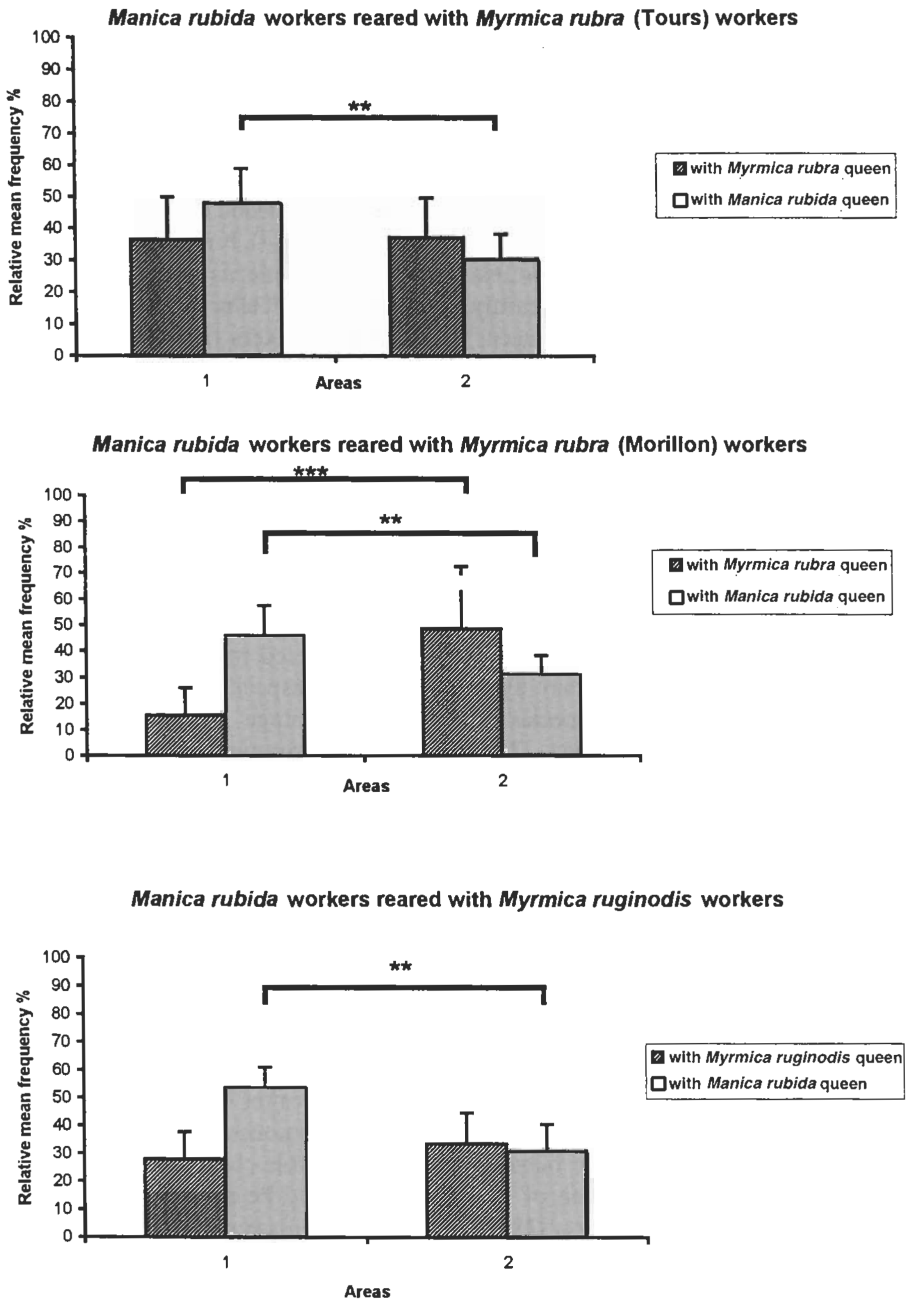


Fig. 8: Choice of aggregation of *Manica* workers reared in heterospecific groups around an allo- and conspecific queen (1, *Manica* queen area; 2, *Myrmica* queen area). * $p < 0.01$, ** $p < 0.001$, *** $p < 0.0001$ (sign test). Neutral areas are not represented

The tests of attractiveness of queens to workers showed that, in homospecific groups, most of the workers remained near a conspecific queen even if she was unfamiliar. This suggests that the queens emit a species-specific pheromone. Moreover, Brian (1986) demonstrated, in three *Myrmica* species, that workers aggregate preferentially around a conspecific queen, but that they cannot discriminate between unfamiliar and familiar conspecific queens. This was also seen in *M. rubra* where workers are attracted as much by unfamiliar queens (from neighbouring nests) as by their own queen (Evesham & Cammaerts 1984), but not in *Linepithema humile* where workers could discriminate non-nestmate queens from their nestmate queens to which they were significantly more attracted (Keller & Passera 1989). In *Cataglyphis cursor*, unfamiliar queens also attract workers (Berton et al. 1991). The hypothesis of a species-specific attractive pheromone has been also presented for *Cataglyphis iberica* by Dahbi & Lenoir (in press) who found different cuticular hydrocarbon profiles according to the caste.

We observed that workers remain in 'queen areas' more frequently than in 'neutral areas', suggesting that all queens emit a non-species-specific odour which is attractive to workers. The study of heterospecific groups pointed out that the queen stimulated workers in brood care. This phenomenon occurred independently of the species of the queen, even with an allospecific queen, adding evidence of a nonspecific effect of the queen signal.

Workers from heterospecific groups were attracted more by an unfamiliar queen of the familiar species than by an unfamiliar conspecific queen. The cohabitation of workers of both species from the pupal stage inhibited the natural attraction to a conspecific queen. The early social environment appeared to be, for our species, a crucial factor in the elaboration of an adult's recognition criteria. This sensitive period was previously identified as important for the development of queen/worker relationships in *Myrmica* (Brian 1986) and *Cataglyphis* (Berton et al. 1991).

Individuals of the genus *Myrmica* appear to be more easily influenced by their social environment than *Manica* individuals. The latter appear more rigid, with less capacity for early learning, which confirms our previous results that for *M. rubida* species, the genetic factors determining the behaviour of recognition in adults are more important than environmental factors encountered just after emergence (Vienne et al. 1995).

We cannot say that the queen directly controls worker behaviour in the same way she inhibits their ovarian development with pheromones. However, the queen is a factor in maintaining the behavioural and heritable characters of a species, and in promoting the cohesion of the colony. It could be possible as previously stated by Hölldobler & Wilson (1990) that workers answer to the presence of a queen in such a way as to increase their own inclusive fitness. This hypothesis can be supported by Cole (1986) who observed in queenless groups of *Leptothorax allardycei* that the most competitive workers spend more time on dominance exchanges than in brood care. The queen should emit a signal to focus the attention of workers on brood to promote the survival of the colony. It is well known that the queen controls worker fertility by pheromones. Keller & Nonacs (1993) argued that queen pheromones are honest, evolutionary stable signals indicating both the queen's presence and level of fecundity. The workers' response to queen signalling is therefore sterility (see Bourke & Franks 1995 for discussion). According to our results we can assume that the workers' response is not only physiological but also behavioural and affects all the activities of the colony, particularly brood tending.

Acknowledgements

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