

SOCIAL BEHAVIOUR DURING NEST-MOVING IN THE ANT *MYRMICA RUBRA* L. (Hym. Form.)

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SUMMARY

The colony-moving of *Myrmica rubra* L. was induced in the laboratory by worsening the microclimate of the nest.

A detailed analysis of the whole process is given; it is based both on observation and on traffic measurements between the old and the new nests. Three periods can be recognized: exploration, emigration, and final exploration. Two recruitment methods occur, initiated by distinct motor displays: group recruitment takes place first, whilst carrying behaviour becomes the main technique later.

The organization of the group is described. The recruiter extrudes its sting while returning to the old nest and while leading the group. Tracks left on soot-coated glasses are analyzed. Sticks crushed with either the poison gland or the Dufour's gland are effective in leading the ants.

Most adult carrying postures are typical for myrmicines: the occurrence of atypical postures is discussed. All the carrying acts (of brood and adults) are effected by 25 % of the workers (on average); carrying activity is age-dependent. The stability of the group of carriers is tested during successive emigrations.

Social regulation potentiality is strong: even queens or callows can move with their larvae when isolated from the rest of the colony.

RESUME

Etude du comportement social lors du déménagement chez la fourmi *Myrmica rubra* L. (Hym. Form.)

Le déménagement de sociétés de *Myrmica rubra* L. a été induit en laboratoire en dégradant le microclimat des nids.

L'analyse détaillée du processus de déménagement s'appuie sur l'observation et sur la mesure du trafic entre l'ancien et le nouveau nid. On distingue trois phases: l'exploration, l'émigration, et l'exploration finale. *Myrmica rubra* utilise deux modes de recrutements initiés par des comportements d'invitation distincts: les recrutements de groupe dominant au début, les transports par la suite. L'organisation du groupe est étudiée. Le « leader » émet une phéromone issue de l'appareil à venin. Nous avons tenté d'en préciser l'origine glandulaire (glande de Dufour ou glande à poison) par des expériences de leurre et l'analyse de traces sur du noir de fumée.

La plupart des transports se font selon la position typique des myrmicines ; la signification des transports atypiques est discutée. Le transport de compagnes ou de couvain est effectué par 25 % des ouvrières (en moyenne), dont la majorité montre une forte pigmentation cuticulaire. La stabilité de ce groupe d'ouvrières transporteuses est testée au cours de déménagements successifs.

Le pouvoir de régulation sociale est élevé : des reines ou des jeunes ouvrières isolées du reste de la colonie peuvent mener un déménagement à bien.

INTRODUCTION

Nest-moving in ants is a primordial social event as it is essential for the survival of the colony whenever the ecological conditions change too drastically. For example, during the severe summer drought of 1976, numerous nest-movings of *Myrmica rubra* were observed near Brussels. Moreover, C. DE VROEY (personal communication) observed colonies of *M. rubra* driving away alien colonies of the same species or being dragged away from their nest by an expanding *L. niger* society.

Moving is a highly organized social activity, which involves the entire colony. It constitutes therefore a good opportunity for studying social behaviour.

If we exclude the peculiar case of the daily migrations of army ants, complete detailed descriptions of nest-movings have only been given recently for several species of *Leptothorax* (MÖGLICH, 1978). Usually, the studies turn on particular aspects of emigration, such as recruitment, carrying behaviour and division of labour (HÖLLDOBLER, 1971 ; MÖGLICH, 1973 ; MÖGLICH and HÖLLDOBLER, 1974 ; MEUDEC, 1976, 1977).

Myrmica rubra L. (= *Myrmica laevinodis* Nyl) was chosen for this study because its social behaviour has been already studied in other circumstances : food recruitment (CAMMAERTS, 1978, DLUSSKY, 1978) alarm (CREWE and BLUM, 1970), defence (CAMMAERTS, 1975, DE VROEY and PASTEELS, 1978), brood-rearing (BRIAN, 1974). Moreover, *M. rubra* is known to move often in natural conditions, at least when the colonies are small (DOBZANSKA and DOBRZANSKI, 1976).

MATERIALS AND METHOD

Our experimental societies contain around 100-200 workers, 1-5 queens, 60-100 larvae and nymphs, and 20-200 eggs. These societies were obtained by dividing large laboratory colonies. According to WEIR (1958), the exit of ants caused by graded disturbances is a function of their polyethism. In order to get balanced experimental colonies, the workers were equally distributed as soon as they left their nest, the latter being tapped repeatedly. Finally, the nest was opened, and the remaining ants were also distributed.

Emigrations were induced in the laboratory by worsening the microclimate of the nest, and providing the ants with a more suitable nest at a distance of about 75 cm. The factors inducing movement were chosen according to the known facts of the biology of the species (Table I). The resulting experimental set-up is illustrated on figure 1.

Table I. — Laboratory conditions inducing nest-moving in *Myrmica rubra*.
Tableau I. — Conditions expérimentales utilisées pour induire les déménagements.

Factors inducing nest-moving	Biology of <i>Myrmica rubra</i>	Nest conditions	
		Old nest	New nest
1. Drought	Preference for damp places (meadows-sparse woodland)	No water is provided for about 10 days before experiment	Well humidified
2. Light	Preference for shadowed places ; No vision of red colour	A 60 Watt bulb about 30 cm distant from the nest is switched on, providing the nest with a light of 44,000 Lux	Red cellophane covers the nest ; inside luminosity : 88 Lux
3. Temperature	<i>Myrmica rubra</i> lives in a temperate climate	The light causes a 6-7° temperature increase in the nest	± 21°
4. Lack of confinement	Thigmotactism	Nest-space more than 1 cm high	Nest-space about 0.3 cm high

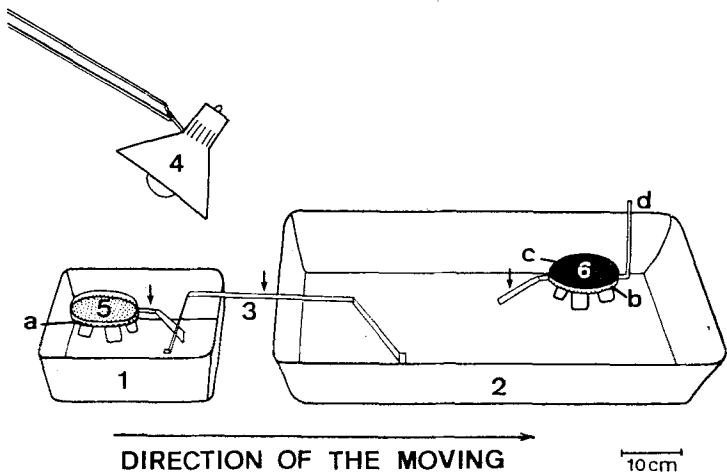


Fig. 1. — Experimental set-up.
1 and 2: polyvinyl chloride areas ; 3: cardboard bridge ; 4: 60 Watt bulb ; 5 and 6 : Petri dishes : " old " and " new " nests ; a: thin layer of plaster of Paris ; b: thick layer of plaster of Paris ; c: red cellophane ; d: water-providing tube.
The arrows indicate the three places where the passing ants were counted.

Fig. 1. — Dispositif expérimental.
1 et 2: bacs en chlorure de polivinyl ; 3: pont en carton ; 4: lampe (60 Watt) ; 5 et 6: boîtes de Petri : « ancien » et « nouveau » nids ; a: fine couche de plâtre de Paris ; b: couche épaisse de plâtre de Paris ; c: cellophane rouge ; d: tube pour l'humidification du plâtre.
Les flèches indiquent les trois emplacements de mesure du trafic des fourmis.

For marking the ants, little spots of silver lacquer of different shapes were placed on different parts of their body. Usually the ants kept these marks for at most 10 hours. When long term marks were necessary, the petiole was surrounded with a thin copper thread (DOBZANSKI, 1966).

RESULTS

1. — Temporal organization of the nest-moving

Five movements were analysed from beginning to end. We recorded the traffic of the ants in each direction during successive time lapses of two min. These measurements were taken at three different places indicated by the arrows on figure 1. Figure 2 gives the results obtained for one typical movement: the traffic measurements are plotted along the time; the moment at which the bulb is switched on, and at which the new nest is provided is considered as time zero (about 9 a.m.). Figure 3 shows the settlement in the new nest during the movement illustrated in figure 2. The workers' settlement in the new nest was calculated from the traffic measurements, while brood settlement was deduced from the number of ants which carried the brood. This last measurement is thus an approximation since one ant may carry several eggs or small larvae. Three successive phases appear clearly :

- a - an exploration period,
- b - an emigration period,
- c - a final exploration period.

a - *Exploration period*

The first period is characterized by a very low traffic at the three locations. Only a few scouts explore the areas and the new nest. Most scouts do not go far from the nest; if they do, they usually stay for a long time (lost?) in each area. A few hours are usually needed before a first scout may arrive, apparently independently from each other, but usually no more discovers the new nest. Before the beginning of recruitment, up to 20 scouts

Fig. 2. — Organisation temporelle d'un déménagement : mesures du trafic.

A. Trafic à l'entrée de l'ancien nid.

B. Trafic sur le pont.

C. Trafic à l'entrée du nouveau nid.

Pour chaque direction de circulation, on enregistre le nombre de passages durant des laps de temps successifs de 2 min. Les valeurs obtenues sont portées en ordonnée. La ligne continue joint les points correspondant à la direction ancien nid vers nouveau nid; la ligne pointillée correspond à la direction opposée.

In: dernier transport de couvain; t: temps (en heures); t1: premier transport; tn: dernier transport; tr: trafic; ♀: passage de la reine; Final explor.: phase d'exploration finale; →: indiquent les pics correspondant à un même recrutement enregistré aux 3 points de comptage; ...→: indique le pic des retours vers l'ancien nid qui suit chaque pic de recrutement (graph. A).

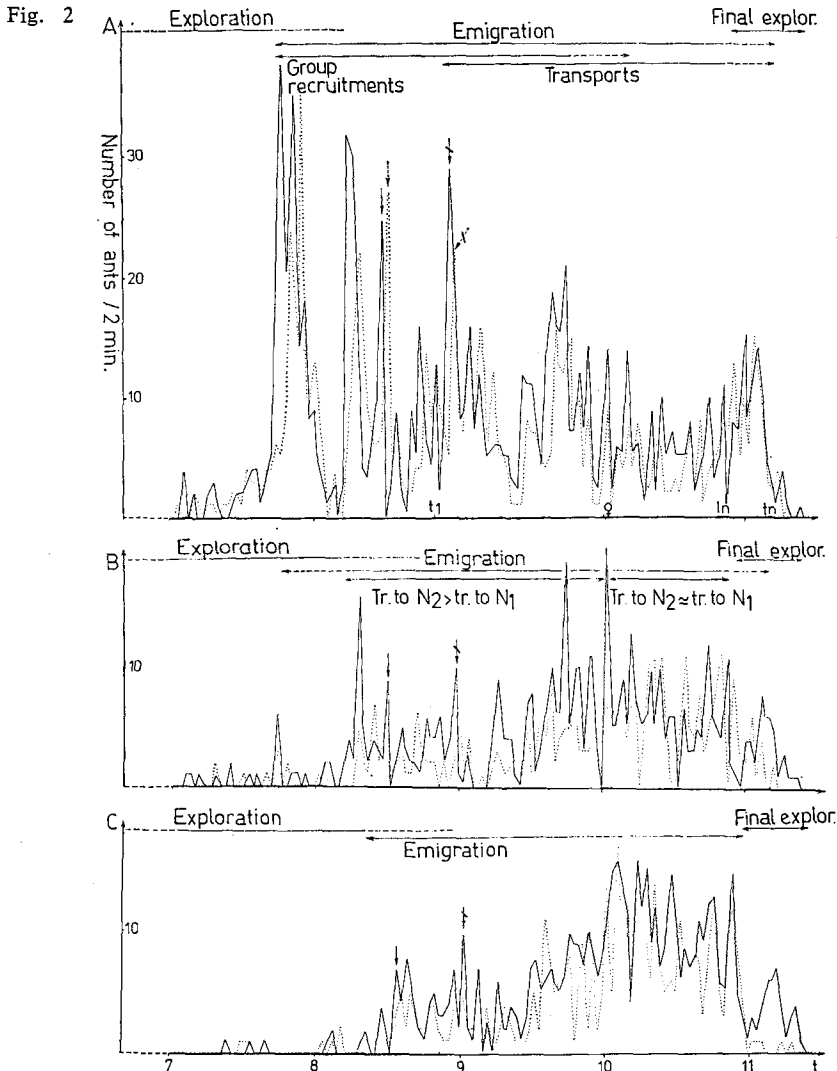


Fig. 2. — Temporal organisation of a movement: traffic measurements.

A. Traffic measurements at the entrance of the old nest.

B. Traffic measurements on the bridge.

C. Traffic measurements at the entrance of the new nest.

For each direction of the traffic, the number of passing ants is counted during successive time lapses of 2 min. The values so obtained are put on the ordinate. The continuous line joins the points corresponding to the direction old nest to new nest. The dotted line corresponds to the reverse direction. In: last brood transport; t : time (in hours); t_1 : first transport; t_n : last transport; tr : traffic; q : queen's going past route; final explor.: final exploration period.

Solid arrows indicate peaks corresponding to the same recruitment act at the three measurement places. In plot A, for each of these peaks, dotted arrows indicate the corresponding peak, for the traffic in the opposite direction.

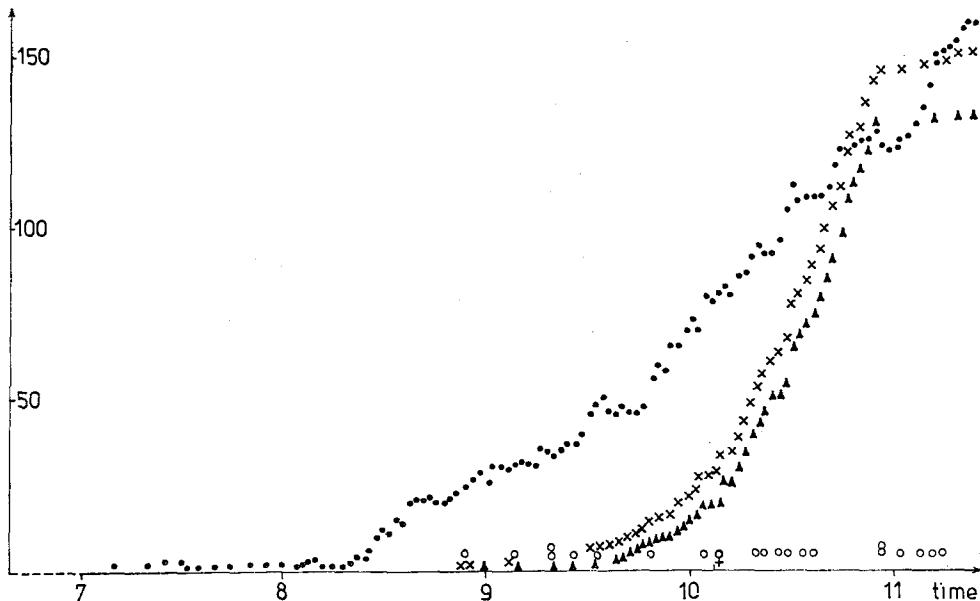


Fig. 3

Fig. 3. — Temporal organization of a movement: settlement of the new nest, and transport to the entrance of the new nest. Same occasion as in figure 2.

Cumulative plots: ●: number of workers; ▲: number of brood carried; ×: total number carried (brood and nest-mates).

○: workers carried; ♀: entrance of the queen.

Fig. 3. — Organisation temporelle d'un déménagement: peuplement du nouveau nid et transports à l'entrée de celui-ci. Ce graphique correspond au même déménagement que la figure 2. Courbes cumulatives: ●: nombre d'ouvrières; ▲: nombre de transports de couvain; ×: nombre de transports total (couvain + compagnes).

○: transport d'ouvrières; ♀: entrée de la reine dans le nouveau nid.

than 5 ants explore the nest at the same time (fig. 3). The scouts remain for a long time practically motionless in the new nest. During their active periods, they walk across the nest. Their exploration is frequently interrupted by self grooming; mutual grooming is less frequent. The scouts may or may not explore the neighbourhood of the nest-site before leaving for the old nest. If the scout succeeds in finding its way to the old nest, it often travels back and forth once or a few times between the nests before performing the first effective recruitment. The end of the exploration period is difficult to determine for two main reasons. On one hand, scouts are still exploring the new nest-site when the first recruitment occurs. On the other hand, even recruited ants may explore the new nest before they start recruiting themselves.

b - Emigration period

This stage is characterized by an intense traffic at each level (fig. 2 A, B, C.), and the settlement in the new nest is important (fig. 3).

The emigration period starts with the first high peak of traffic. Such a peak corresponds to the passage of a group of ants, which results from an effective recruitment.

The height of peaks corresponding to the passage of the same group at the three points of observation decreases roughly from plot 2 A to plot 2 C : Two examples are given by the solid arrows on these plots. The recruitment method is thus not very effective. This can be explained by considering plot 2 A : each traffic peak corresponding to the direction towards the new nest (e.g. those indicated by solid arrows) is immediately followed by a traffic peak corresponding to the opposite direction (broken arrows). Most of the ants lose their leader ; then, either they return to the old nest, or they finally reach the new nest by themselves. This is probably the reason why the nest settlement does not show the discontinuous growth which could have been expected of group recruitments.

The height of the peaks, and thus the effectiveness of the recruitment, decreases with time (fig. 2 A). Brood and adult transportation begins about one hour after the first group recruitment, and increases sharply one half hour later (fig. 3).

From about the tenth hour, most of the ants travelling back and forth are carriers, and the traffic in both directions is about equal. This is particularly evident at the level of the bridge (fig. 2 B).

Two somewhat overlapping phases may thus be distinguished in the emigration period :

- a group recruitment period,
- a transportation period.

The overlapping between both periods may be as important as in the example of figure 2, but they may sometimes be much more clear-cut. During the transition period, one ant may both carry, and lead nest-mates.

The number of transportations per unit of time increases during the emigration period (fig. 3). This indicates that the number of carriers or (and) their activity grows with time ; this will be discussed later. There are no distinct phases of transport for the brood and the adults, which were both carried in no apparent order (fig. 3). The moment at which the queens migrate (either being carried, or by themselves) varies greatly from one moving to the other, but always occurs well within the emigration period.

c - Final exploration period

After the emigration, the old nest, and, to a lesser extent both areas, are still explored for some time. This short period is shown on the plot 2 A

by an increasing traffic at the entrance of the old nest, while no, or very few, nest-mates or brood are left in the nest.

In our experimental conditions, the emigration periods lasted from 90-620 min, most of them lasting between 150-300 min. The final exploration period never lasted more than 20 min. The duration of the exploration period is far more difficult to evaluate. In our experiments, 1-10 hours passed between the moment at which the new nest was provided and the first recruitment.

2. — Group recruitment behaviour

The first action of a recruiter coming back in the old nest is usually a short bout of self-cleaning. The ant stops however, and performs an invitation behaviour, which consists in a motor display characterized by very short and fast runs. This behaviour is mostly directed towards groups of ants, instead of towards single individuals. Some workers are jostled as a result.

The recruiter's mandibles remain wide open during the whole process.

Numerous nest-mates immediately answer by running all over the nest, their antennae being more or less erect. Some gather near the exit. After 10-30 sec the recruiter suddenly leaves the nest. It is then followed by a varying number of nestmates. When the invitation behaviour is very effective, the group of ants may consist of up to 40 individuals.

A few observations suggest the intervention of a chemical signal during the invitation behaviour. Not all the recruited ants have been encountered by the recruiter. Moreover, some recruitments are effective without any motor display being performed.

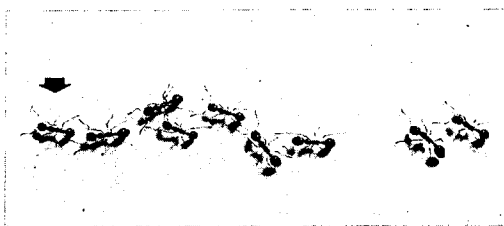


Fig. 4

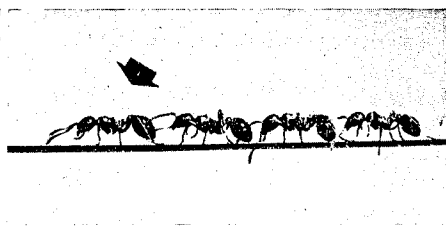


Fig. 5

Fig. 4 et 5. — Groups of recruits lead by the recruiter (arrow).

Fig. 4 and 5. — Recrutement de groupe; la flèche indique l'ouvrière-guide.

Fig. 6. — Leader of a group with its sting extruded (arrow).

Fig. 6. — Fourmi guidant un groupe; la flèche indique son aiguillon.



Fig. 6

Figures 4 and 5 illustrate typical groups of workers following a leader. The recruiter, which always leads the group, is characterized by its often extruded sting (fig. 6). The recruits follow the leader at a distance of a few mm to about 1 cm; bodily contacts are very fleeting and appear to occur by chance only.

As shown by the traffic measurements, the cohesion of the group is not very strong. Although a few tens of ants may have left the nest following the leader, the group consists of no more than 2-10 nest-mates at the level of the bridge, the small groups being far more numerous than the large ones (fig. 7). The recruiter is often quite alone. The dislocation of the group always seems to correspond to a hesitation of the leader, whose sting is then retracted. While entering the new nest, the leader is usually followed by no more than 5 nest-mates. Several among them were not recruited in the old nest; they have encountered the leader by chance, and have followed it. Some ants wandering in the area may follow a recruiter on its way towards the old nest. The cohesion of such groups is weak; the ants follow the leader for only a short distance, leaving it one by one.

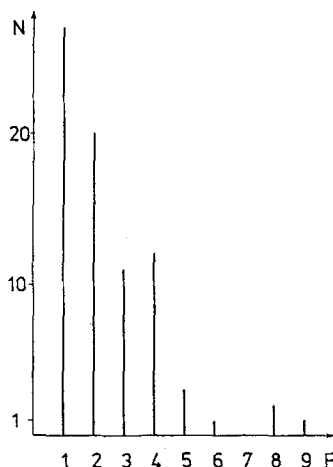


Fig. 7. — Size of the groups. F: number of followers; N: number of groups of each size. The groups were observed at the level of the bridge during nine emigrations.

Fig. 7. — Effectif du groupe (mesuré au niveau du pont). F: nombre de fourmis guidées. N: nombre de pelotons observés.

The lack of physical contact between the leader and the recruits strongly suggests that the latter perceive an attractive pheromone emitted by the leader. The frequent extrusion of the recruiter's sting suggests that the leading pheromone is produced by the poison apparatus (fig. 6). Sticks of wood with either a poison gland or a Dufour's gland crushed on their tip may both be used to guide the workers towards the new nest. However, our experiments do not allow us yet to decide which pheromone(s) is (are) emitted by the leader.

The sting of the recruiter is not only extruded when it leads the group, but also during its way back to the old nest. This behaviour corresponds

probably to the production of an orientation signal. In our experimental conditions, the chemical orientation was not very effective: numerous ants (recruiters or recruits) were lost. However, the existence of a trail may be demonstrated by the following stratagem. A slat was laid as a guide line between the bridge and the new nest during the emigration period; it was moved away after a few hours. The ants then went on travelling on the "pass" that was determined by the slat. We may thus assume that each recruiter lays an orientation pheromone; but to be effective, the trail has to be reinforced by numerous deposits.

In order to get a better understanding of these pheromone emissions, the method previously described by HANGARTNER (1969) was used. A soot-coated glass plate was laid on the bridge. The tracks left by the crossing ants were analysed. Typical slides were used as negatives for photographic enlargements (fig. 8). The observed tracks were of the four types already described by HANGARTNER (1969) in *Solenopsis geminata* Fabr.:

- Tracks of tarsae alone.
- Tracks of tarsae + abdominal setae.
- Tracks of tarsae + abdominal setae. + sting.
- Tracks of tarsae + sting.

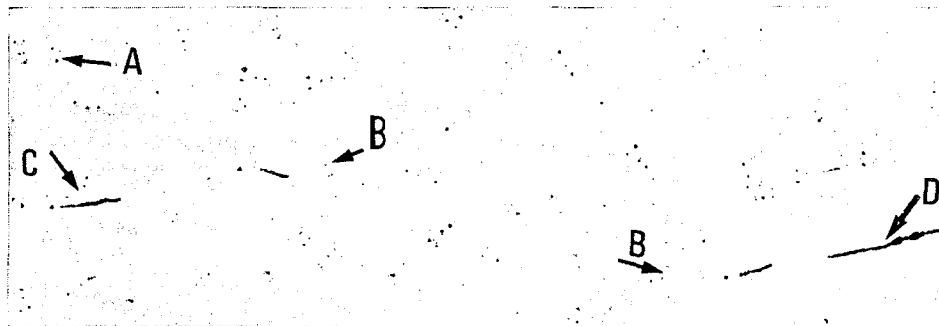


Fig. 8. — Tracks left on a soot-coated glass by a recruiting ant going towards the new nest-site.

A: tracks left by the tarsae; B: tracks left by the abdominal setae; C: combined tracks (abdominal setae + sting); D: tracks left by the sting.

Fig. 8. — Traces laissées sur une plaque de verre noircie à la fumée, par une fourmi recruteuse se dirigeant vers le nouveau nid.

A: traces de tarses; B: traces des soies abdominales; C: traces mixtes (soies + aiguillon); D: traces d'aiguillon.

Scouts, lost and recruited ants, as well as recruiters at the end of the final exploration period, left type A tracks: they probably do not lay any chemical signal. During the emigration period, recruiters or carriers always left type B, C. or D tracks, whatever the direction of their crossing. Type B

tracks are very short : their length lies between 0.12 and 1.40 mm. Their frequency varies greatly : during a single crossing of one ant, the tracks may be a few cm apart, or quite close to each other. Sting tracks, either of type C or D, are less frequent than setae B tracks, and always intermixed with them. Their length varies between 0.12 and 2.40 mm.

3. — Social carrying behaviour

The carrying act is initiated by an invitation behaviour which recalls the one observed during group recruitments. The amplitude of the movement is weaker, and it is more directed towards one larva or one ant, instead of towards groups of ants. It looks thus more like a jerk than like a run.

This motor display is usually observed in the old nest during the transportation period. However, it may be performed towards ants which stay motionless in the area, and it often occurs during the final exploration period. In the latter case the ants address the jerks to any worker encountered, even to former carriers, and the jerks may also be effected without any nest-mate being present ; this demonstrates the high motivation level of the former carriers which have not found another load.

Eggs, larvae or pupae are quickly seized after a few jerks. No order appears in the transport of the brood : the carrier indifferently choses a group of eggs or larvae of first instar, one more mature larva, or one pupa. A nest-mate is first slightly pulled about ; antennal contacts occur, and the jerks may start again. The invited ant then usually folds its antennae, and flexes its legs. The carrier grasps it at the head (" neck ", or " cheeks ") or less frequently at the prothorax. The right orientation of the carried ant is obtained by successive adjustment of the grip. The carried ant immediately answers by flexing its gaster above its nest-mate's head, in a typical myrmicine carrying posture (fig. 9). If a nest-mate does not answer to the motor display, the carrier may seize the non-responding worker the best it can, with the result that the carrying posture is atypical (fig. 10). Such atypical postures often occurred when very young ants were carried.

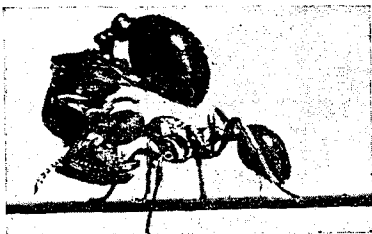


Fig. 9. — Typical carrying posture (queen carried).

Fig. 9. — Transport d'une reine selon une position typique.

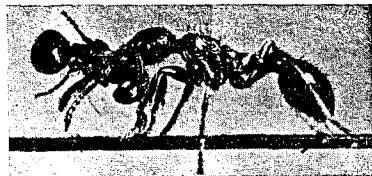


Fig. 10. — Atypical carrying posture ; The arrow indicates the extruded sting.

Fig. 10. — Transport d'ouvrière selon une position atypique ; la flèche indique l'aiguillon de la fourmi qui transporte.

While carrying a load, the ant usually extrudes its sting (fig. 10), and sometimes guides a few recruits.

During 6 nest-movings, 143 ants, or 23.0 % of the whole worker population was carried.

4. — Polyethism

1° - Worker polyethism

Because carrying ants are easier to identify quickly than recruiters, we mainly studied polyethism in carrying behaviour.

During 8 nest-movings performed by 5 different colonies, the percentage of carriers ranged from 18 % to 34 %, with a mean of 25 % (219 out of 878 workers).

Table II. — Distribution of carrying ants among different age categories.

Tableau II. — Répartition des ouvrières transporteuses parmi les différentes classes d'âge.

AGE CATEGORIES													
	1 and 2			3			4			5			un- know (2)
col.	C	N	C/N	C	N	C/N	C	N	C/N	C	N	C/N	C
1	—	25	0 %	6	43	14,0 %	20	47	42,5 %	1	2	50,0 %	2
1* (1)	—	20	0 %	5	40	12,5 %	17	45	37,8 %	4	6	66,7 %	3
2	—	21	0 %	1	21	4,8 %	22	52	42,3 %	4	9	44,5 %	3
2*	—	21	0 %	5	30	16,7 %	16	42	38,1 %	1	4	25,0 %	—
3	—	20	0 %	—	25	0 %	17	51	33,4 %	4	14	28,6 %	2
3*	—	25	0 %	1	22	4,6 %	9	42	21,4 %	8	17	47,1 %	1
4	—	34	0 %	12	59	20,3 %	15	43	34,9 %	—	1	0 %	7
5	—	2	0 %	—	10	0 %	15	65	23,1 %	9	20	45,6 %	9
Σ	—	168	0 %	30	250	12,0 %	131	387	33,3 %	31	73	42,5 %	27
<div><div>χ²</div><div><div>p < .0005</div><div>.15 < p < .25</div><div>p < .0005</div></div></div>													

N: total number of ants in each age category.

C: number of carriers.

Col.: colonies.

(1) The asterisk indicates a second movement induced with the previous colony.

(2) The age category of the carriers were observed after the end of the movement; some of them, having lost their mark, were not identified.

N: nombre total de fourmis pour chaque classe d'âge.

C: nombre de fourmis actives.

Col.: colonie.

(1) L'astérisque indique qu'il s'agit d'un second déménagement induit avec une même colonie.

(2) La classe d'âge des transporteuses a été observée après le déménagement; certaines ayant perdu leur marque, ne purent pas être identifiées.

The carrying activity is age-dependent (Table II). This could be determined by sorting the ants into five broad age categories according to their pigmentation (CAMMAERTS-TRICOT, 1974 a). No young ants (pigmentary groups 1 and 2) ever carried, and more carriers were encountered among the groups 4 and 5 than among younger ants belonging to group 3. No significant difference could be observed between the proportions of carriers among the ants belonging to the group 4 and 5.

A considerable variation in the individual activity was observed amongst the carriers, a minority of individuals made most of the transports. During one experiment, 27 workers effected 121 carrying acts, among which 75 were performed by only 5 workers (fig. 11). This figure illustrates also that there is apparently no specialization in the transport of either brood or adults.

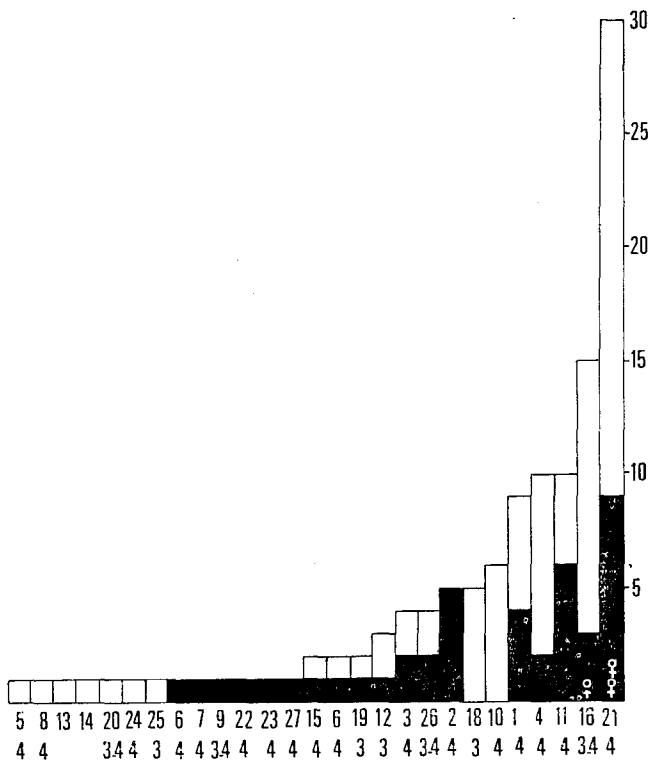


Fig. 11. — Each column of the sociogram represents the number of carrying acts performed by one carrier of the colony. The number attributed to each individual ant, and its age category are indicated under each column. In black: nest-mate transport; in white: brood transport. ♀: queen transport.

Fig. 11. — Sociogramme montrant le nombre de transports effectués par chaque ouvrière active, au cours d'un déménagement. Le numéro attribué à chaque fourmi, et sa classe d'âge sont précisés sous les colonnes. En noir: transport d'ouvrière; en blanc: transport de couvain; ♀: transport de reine.

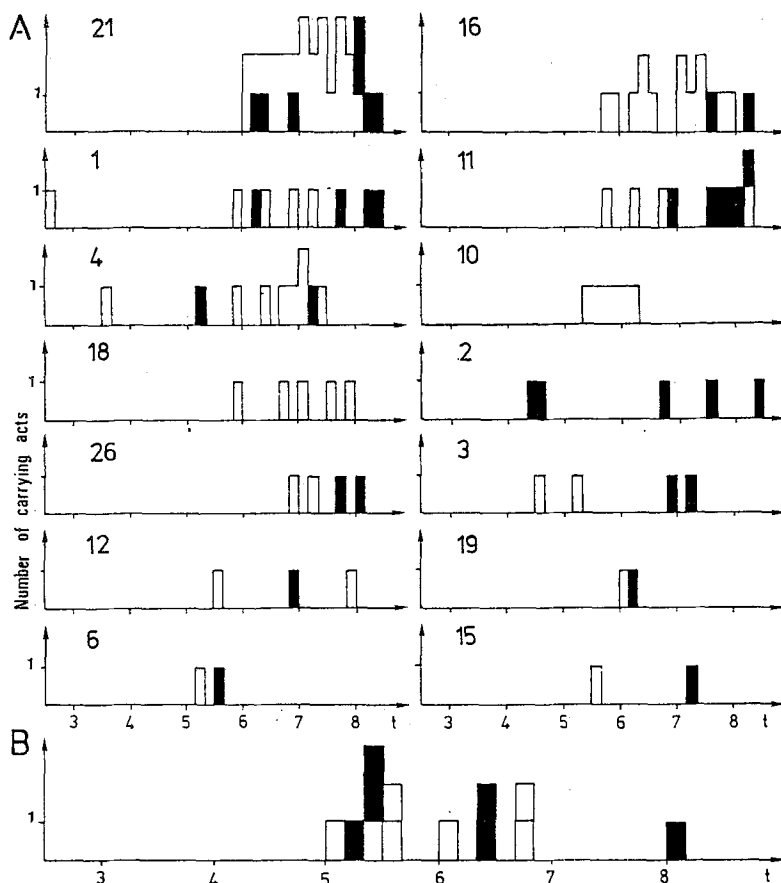


Fig. 12. — Individual carrying activity during time (t, in hours). Same moving as in figure 11; the number designate the same individual ants in both figures. In black: adult transport; in white: brood transport.

A. Individual activities. The sequence of the transports in one column must be read from bottom to top.

B. Combined activity of all the workers which only carried once.

Fig. 12. — Activité individuelle de transport au cours du temps (t, en heures). Même déménagement que la figure 11: les numéros désignent les mêmes individus dans les deux figures. En noir: transport d'adulte; en blanc: transport de couvain.

A. Activité individuelle: la séquence de transports dans chaque colonne doit être lue de la base vers le sommet.

B. Répartition temporelle des transports effectués par toutes les ouvrières qui n'ont amené qu'une seule charge au nouveau nid.

The individual activity through time of all carriers during one movement is given in figure 12; The number of carrying acts made by each ant depends less on the time when activity begins than on an individual rhythm: ants number 12 and 16, which have both begun to carry at about the same time made respectively 3 and 15 transports. The ant number 21 performed

31 carrying acts during approximately the same time lapse. The rythm of one transport every 3 min was maintained for more than one hour!

The activity of the carriers often increases with time (fig. 12: ants number 4,16 and 11). The trail probably becomes more efficient and the knowledge of possible visual landmarks could increase.

To test the stability of the carrying activity, two successive movements were induced with the same colony, at 8-10 days interval. This was performed with three different colonies (Table III). Among the carriers of

Table III. — Stability of the group of specialists among the workers of age categories 4 and 5.

Two movings were induced at 8-10 days interval with three colonies (col.).

Tableau III. — Stabilité du groupe de spécialistes du transport. Pour trois colonies (col.), deux déménagements furent induits avec 8-10 jours d'intervalle.

col.	N	C ₁	C ₂	C _{1, 2}	$\frac{C_1}{N}$	$\frac{C_{1, 2}}{C_2}$	χ^2
					N	C ₂	
1	51	19	21	13	.373	.619	p < .05
2	61	20	15	9	.328	.600	p < .05
3	65	15	16	8	.231	.500	p < .025
Σ	177	54	52	30	.305	.577	p < .0005

N: Number of ants of age categories 4 and 5.

C₁: Number of carriers during the first emigration.

C₂: Number of carriers during the second emigration.

C_{1, 2}: Number of carriers during both emigrations.

The χ^2 tests compare the number of C_{1, 2} among C₂ to the number of C₁ among N.

N: Nombre de fourmis appartenant aux classes d'âge 4 et 5.

C₁: Nombre de fourmis actives pendant le premier déménagement.

C₂: Nombre de fourmis actives pendant le second déménagement.

C_{1, 2}: Nombre de fourmis actives pendant les deux déménagements.

the second emigration, the proportion of the ants which had already carried during the first emigration was significantly higher than would have been expected if they were distributed by chance only among the ants of age categories 4 and 5. Thus the probability for any ant of age categories 4 or 5 to carry during one nest-moving is far higher if it has already participated actively in a previous one. We may conclude that the group of carrying ants is rather stable.

Moreover, the ants that have already worked during a previous emigration are far more active than their nest-mates during a following one: for the three colonies, 30 carriers of the first emigration performed 193 transports during the second emigration, while 38 non-carriers of the first emigration effected 81 transports. This difference is highly significant (p < .0005, χ^2 test).

Ants which carry during the moving are also active when faced with other tasks. Carriers were marked during the moving of four colonies. During the following week, the activity of the ants outside the nest was recorded several times a day. The proportion of marked workers among all the ants which fed or drunk (56.0 %), and that of marked workers among all the ants which foraged (51.2 %), were far higher ($p < .0005$, χ^2 test) than the proportion of marked ants among all the workers of age categories 3, 4 and 5 (26.2 %). Six days after a moving, DE VROEY tested the aggressivity of the carriers against *Myrmica sabuleti* intruders. The carriers effected significantly more seizings than the non-carriers ($p = .006$, WILCOXON test). The carriers are thus more aggressive (DE VROEY, in press).

The age category of most ants carried was recorded during 6 migrations.

- 67 ants carried belong to age categories 1,2 ;
- 37 ants carried belong to age categories 3 ;
- 10 ants carried belong to age categories 4 ;
- 0 ants carried belong to age categories 5.

This distribution is significantly different ($P < .0005$, χ^2 test) from the distribution of the total population into the different age categories (respectively 132, 181, 279 and 52 ants).

b - *Queen polyethism*

During sixteen nest-movings, 51 queens migrated. Most of them followed a leader, or found the new nest by themselves, probably guided by the trail. At the level of the bridge, 18 queen transports were observed ; in all of them, the posture was typical for myrmicines (fig. 9).

c - *Social regulation*

The efficiency of emigration was assessed for unbalanced colonies with one the following composition :

- 20 larvae and 25 workers of age categories 1 or 2.
- 20 larvae and 25 workers of age category 3.
- 20 larvae and 25 workers of age categories 4 or 5.
- 15 larvae and 6 queens.

The efficiency in moving of each of those colonies was compared to that of a control society with a better balanced population : 20 larvae, 1 queen, and 24 workers equally distributed among age categories 1 or 2, 3, and 4 or intermediates between 4 and 5.

To avoid ageing of the ants before the experiments, the migrations were induced only 24 hours after the settling of the nest by the ants. The colonies being not yet firmly established in their nest, the red cellophane was taken away, but no light was switched on.

Each colony was able to move, but the time spent before all the larvae were carried (Table IV).

Table IV. — Time before all larvae were moved to the new nest (for colonies of abnormal composition, and more balanced control colonies). Twenty larvae were present in each colony, except for those composed of queens only, which received 15 larvae.

* Some of the workers may have been older than expected.

Tableau IV. — Temps (en jours) écoulé avant le dernier transport de couvain dans le nouveau nid, pour des colonies de diverses compositions. Chaque colonie comporte 20 larves, sauf celle composée exclusivement de reines, qui en comporte 15.

* A la fin de l'expérience, 5 ouvrières avaient atteint un degré de pigmentation correspondant à la classe 3.

Adult composition	25 Workers of age categories			6 queens	Control : 1 ♀ and 8 ♀ of each category
	1 and 2	3	4 and 5		
Delay (in days) before complete migration	13	9	10		8
	16	4	10	17	4
	(3) *	5	6	14	4
	5	4	4	12	4

The control colony was nearly always the first to move, the colony populated by workers of intermediate age (category 3) moved approximately at the same time. The queens were always the last to move. Paradoxically, the ants of age categories 4 and 5, among which the most active carrying ants are usually recorded, were not the first to migrate when isolated from their younger nest-mates. The explanation can be found in the difference in behaviour during the settling of the "old" nest: while in a balanced colony, or in a colony with workers of age category 3, the workers soon gathered the scattered larvae, in a colony with only older workers, the larvae were left for a long time alone. This behavioural difference is still observed when the new nest is provided: the older ants discovered the new nest very soon, but they only took care of the larvae after a rather long time. The reverse is observed for the colonies where only young ants are present. The ants stayed near the brood, and spent a long time before discovering the new nest. The time spent before the end of the migration thus depends highly of the cohesion of the society.

Not only did the queens migrate, but they carried the larvae, although it took a rather long time. However, they never extruded their sting or displayed an invitation sequence; they reached the new nest independently. Their ability to move was highly variable: in all three experiments 2-3 queens died, and some of the surviving queens did not participate in the transport of the brood.

DISCUSSION

The traffic measurements clearly indicate that nest-moving in *Myrmica rubra* is organized in three distinct periods: exploration, emigration, and final exploration.

We do not know if the ants mark the new nest during their first exploration, and this possibility should be investigated.

It was reported that *Myrmica rubra* marks any newly discovered area with a secretion issued from the Dufour's gland (CAMMAERTS *et al.*, 1977). This secretion has a recruiting effect which does not last for more than 3 min, and also a long lasting marking effect. The brief recruiting effect could not be very effective in our experimental conditions, the scout ants being very few at the level of the new nest. The longer lasting effects of this secretion, however, could play a role in determining when the scouts will leave the newly discovered nest, and begin to recruit.

The final exploration of the old nest could be considered simply as the prolongation of the emigration period, corresponding to the time needed by the ants for getting the information that all the brood has been moved. However, such exploration could be quite functional in natural conditions: as the structure of the nest is then more intricate, adults and brood could be left behind. Besides, in an unlimited area, more ants could get lost around the nest.

During the emigration, two more or less overlapping phases can be distinguished. During the first, group recruitments are performed, while carrying behaviour is the main activity in the second.

Two distinct recruitment mechanisms occurring in two somewhat different phases have been described in several species of *Leptothorax* (MÖGLICH, 1978). During the first phase, only tandem recruitments were observed; the recruits later recruit themselves either by tandem running or by transport.

Group recruitment was already observed during foraging in *Myrmica rubra* (EIDMANN, 1927; CAMMAERTS, 1977; DLUSSKY *et al.*, 1978). It is also known to occur during nest-moving in *Camponotus socius*, (HÖLLDOBLER 1971). According to the description given by CAMMAERTS, the invitation behaviour of *M. rubra* appears to be similar in both moving and foraging. Possible differences could only be detected by more refined techniques. On the other hand, the invitation behaviour seems to differ in several aspects between *C. socius* and *M. rubra*. The recruiters perform brief runs in both species, but in *M. rubra*, the wagging and jerking vibrations described for *C. socius* have not been noticed. Moreover, in *C. socius*, the first invitation is very similar to those observed during food recruitment, the motor display changing later from a wagging to a jerking movement. In *M. rubra*, no clear evolution of the invitation behaviour was observed. Also, in *M. rubra*, the invitation behaviour is never followed by the aggregation of nest-mates

around the recruiter as described for *C. socius*. Our observations however, suggest that a chemical signal is involved in the invitation behaviour, since are often alerted without having been in contact with the recruiters. The opening wide of the mandibles during the whole invitation sequence suggests that alarm pheromones from the mandibular glands could be released at that time.

According to CAMMAERTS (1977), the recruiter emits the Dufour's gland pheromone while leading a group towards the food, and a trail pheromone issued from the poison gland when coming back to the nest. She supports this conclusion by relating the aspect of tracks left by the ants on smoked glasses, and the glandular origin of the pheromones emitted. The tracks left by the tip of the abdomen while leading a group are short and regularly spaced, in contrast to those left when laying a trail, which are much longer and continuous (CAMMAERTS-TRICOT, 1974 b). The tracks observed during nest-movings do not fit well into those categories. The relation between the aspect of the tracks and the glandular origin of the chemical cues may thus not be transposed to the very different context that is nest-moving.

Transport is used as a secondary means of worker recruitment and about 20 % of the colony is carried to the new nest. The importance of this recruitment technique is low when compared to *Formica fusca* (MÖGLICH and HÖLLDOBLER, 1975), and *Leptothorax* species (MÖGLICH, 1978), in which most of the ants are carried to the new nest. Nest-mates are usually carried all the time during the emigration period, but in some movements, most were carried after the brood. This is at variance with the results obtained by LANE (1977) in *Leptothorax unifasciatus*, where nest-mates are carried before the brood, and the queen is moved last. In our experimental conditions, no ordering was noticed during brood transport. This is not in accordance with the observations of LE MASNE (1953) in *Ponera eduardi*, in which eggs, larvae and pupae are carried successively. LE MASNE suggests that this could be a general feature in ants according to the observations of other authors with other species. Most of these observations, however, were made in emergency situations, rather than in organized movings.

In *Myrmica rubra*, one ant appears to carry indifferently a nest-mate or a larva. ROSENGREN (1971) reports that in *Formica rufa* the ants which carry larvae and those which carry nest-mates belong to slightly different categories. However, the circumstances were also somewhat different: the transports were made between two permanent nests, not from an old into a new one.

During the movement, all the carrying acts were effected by only 18-34 % of the workers. This activity is age-dependent. The majority of the carriers were found among the most pigmented workers, whereas no callows worked. However, individual activity varies greatly among the carriers, and most of the carrying acts were made by only a few ants. During successive emigrations, the group of carriers, and in particular the most active ants among them, seems to be rather stable. Specialisation is not so strong as it is in

some other species: in *Formica fusca*, a few workers (sometimes 2 or 3) perform all the transports (MÖGLICH and HÖLLDOBLER, 1975). In *Tapinoma erraticum*, however, the percentage of active ants may reach 70 % (MEUDEEC, 1977).

Social regulation potentiality is very strong: even queens or callows are able to move with their larvae when isolated from the rest of the colony. It seems to be more important than in some other species: in *Formica sanguinea* and *Camponotus sericeus* (MÖGLICH and HÖLLDOBLER, 1974), removing the group of recruiting ants considerably increases the time needed for migration. Moreover the colonies were almost unable to achieve an organized emigration when the group of replacement movers was removed in its turn.

That callows are able to carry brood has already been shown in other species (MEUDEEC, 1976). Though, it would be interesting to see if recruitment acts are performed by those callows in which only the Dufour's gland could produce recruitment pheromone. Indeed, no trail pheromone can be detected in their poison gland (CAMMAERTS-TRICOT and VERHAEGHE, 1974) and they do not repond to the mandibular gland secretion (CAMMAERTS-TRICOT, 1974 a).

At first sight, it may appear astonishing that queens are able to migrate with their larvae. However, queens of *M. rubra* often show a high degree of autonomy when placed in extreme conditions: after a long period of starvation, they may leave the nest to eat or drink. This could be linked to the fact that *M. rubra* is a rather primitive myrmicine, in which the polymorphism is low. However, no recruiting behaviour made by a queen has been observed. This could be related to the lack of trail pheromone production (PASTEELS and VERHAEGHE, 1974). Among queens, the capacity to emigrate and carry larvae seems to vary from one individual to another. This variability may be age-dependent, but the individual behaviour of queens in polygynous societies remain to be more closely analysed.

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References

- BRIAN M.V., 1974. — Brood-rearing behaviour in small cultures of the ant *Myrmica rubra* L. *Animal Behav.*, 22, 879-889.
- CAMMAERTS M.C., 1977. — Recrutement d'ouvrières vers une source d'eau pure ou sucrée chez la fourmi *Myrmica rubra* L. (Formicidae). *Biol. Behav.*, 2, 287-308.
- CAMMAERTS M.C., MORGAN E.D., TYLER R., 1977. — Territorial marking in the ant *Myrmica rubra* L. (Formicidae). *Biol. Behav.*, 2, 263-272.
- CAMMAERTS-TRICOT M.C., 1974 a. — Production and perception of attractive pheromones by differently aged workers of *Myrmica rubra* L. *Ins. Soc.*, 21, 235-248.
- CAMMAERTS-TRICOT M.C., 1974 b. — Recrutement d'ouvrières chez *Myrmica rubra* L. par les phéromones de l'appareil à venin. *Behaviour*, 50, 111-122.
- CAMMAERTS-TRICOT M.C., 1975. — Ontogenesis of the defense reactions in the worker of *Myrmica rubra* L. (Hymenoptera, Formicidae). *Anim. Behav.* 23, 124-130.

- CAMMAERTS-TRICOT M.C., VERHAEGHE J.C., 1974. — Ontogenesis of the trail pheromone production and trail following behaviour in the workers of *Myrmica rubra* L. (Formicidae). *Ins. Soc.*, 21, 275-282.
- CREWE R.M., BLUM M.S., 1970. — Alarm pheromones in the genus *Myrmica* (Hymenoptera, Formicidae). *Z. Vergl. Physiol.*, 70, 363-373.
- DE VROEY C. — Mesure de l'agressivité chez *Myrmica rubra* (= *Myrmica laevinodis*, Formicidae). *Biol. Behav.* (In press.)
- DE VROEY C., PASTEELS J.M., 1978. — Agonistic behaviour of the ant *Myrmica rubra* L. *Ins. Soc.*, 25, 247-265.
- DLUSSKY G.M., VOLTZIT O.V., SULKHANO A.V., 1978. — Organization of group foraging in ants of the genus *Myrmica*. *Zool. Z.H.*, 57, 65-77.
- DOBZANSKA J., DOBRZANSKI J., 1976. — The foraging behavior of the ant *Myrmica laevinodis* Nyl. *Acta Neurobiol. Exp.*, 36, 545-559.
- DOBZANSKI J., 1966. — Contribution to the ethology of *Leptothorax acervorum* (Hymenoptera, Formicidae). *Acta Biol. Exp.*, 26, 71-78.
- EIDMANN H., 1927. — Ameisen und Blattläuse. *Biol. Zentralblat.* 47, 537-555.
- HANGARTNER W., 1969. — Structure and variability of the individual odor trail in *Solenopsis geminata* Fabr. (Hymenoptera, Formicidae). *Z. vergl. Physiol.*, 62, 11-120.
- HÖLDOBLER G., 1971. — Recruitment behavior in *Camponotus socius* (Hymenoptera, Formicidae). *Z. Vergl. Physiol.*, 75, 123-142.
- LANE A., 1977. — Recrutement et orientation chez la fourmi *Leptothorax unifasciatus*. Rôle de la piste et des tandems. *Thèse de doctorat*, Dijon.
- LE MASNE G., 1953. — Observations sur les relations entre le couvain et les adultes chez les fourmis. *Ann. Sci. Nat. Zool.*, 15, 1-56.
- MEUDEC M., 1976. — Rôle des stimulations provenant du couvain sur le comportement de transport des nymphes par les ouvrières de *Tapinoma erraticum* (Formicidae-Dolichoderinae). *C.R. Acad. Sci. Paris*, 282, 1041-1043.
- MEUDEC M., 1977. — Le comportement de transport de couvain lors d'une perturbation du nid chez *Tapinoma erraticum* (Dolichoderinae). Rôle de l'individu. *Ins. soc.*, Paris, 24, 345-352.
- MÖGLICH M., 1973. — Communication during nest-moving in ants. *VIIIth IUSI Congr.*, London, pp. 274-278.
- MÖGLICH M., 1973. — Social organisation of nest emigration in *Leptothorax* (Hym., Form.) *Ins. Soc.*, 25, 205-225.
- MÖGLICH M., HÖLDOBLER B., 1974. — Social carrying behaviour and division of labour during nest-moving in ants. *Psyche*, 81, 219-236.
- MÖGLICH M., HÖLDOBLER B., 1975. — Communication and orientation during foraging and emigration in the ant *Formica fusca*. *J. Comp. Physiol.*, 101, 275-288.
- PASTEELS J.M., VERHAEGHE J.C., 1974. — Dosage biologique de la phéromone de piste chez *Myrmica rubra* L. *Ins. Soc.* 21, 167-180.
- ROSENGREN R., 1971. — Route fidelity, visual memory and recruitment behaviour in foraging wood ants of the genus *Formica*. *Acta Zool. Fennica*, 133, 1-106.
- WEIR J.S., 1958. — Polyethism in workers of the ant *Myrmica*. *Ins. Soc.*, 4, 97-125.