

Research article

Individual flexibility and choice of foraging strategy in *Polyrhachis laboriosa* F. Smith (Hymenoptera, Formicidae)

J.-L. Mercier^{1,2} and A. Lenoir²

¹ Laboratoire d'Éthologie Expérimentale et Comparée, Université Paris Nord, UPRES A CNRS 7025, F-93430 Villetaneuse, France
e-mail: jlmercier@univ-tours.fr:

² Present address: Laboratoire d'Éthologie et Pharmacologie du Comportement, Faculté des Sciences et Techniques, Parc de Grandmont, F-37200 Tours, France, e-mail: lenoir@univ-tours.fr:

Received 23 February 1998; revised 15 October 1998; accepted 20 October 1998.

Summary. We report in this study that the tree-dwelling African ant *Polyrhachis laboriosa* (Formicinae) uses different foraging strategies according to the size of the available food sources. We demonstrate that a recruitment behaviour can be induced with a 125 µl alimentary reward and that foraging remains solitary when rewards are smaller. Small rewards do not elicit trail-laying behaviour, and exploration behaviour is considerable. With large permanent food sources, scouts use group recruitment and there is less exploration around the reward. The choice of the foraging strategy is determined by the first forager, which modifies its behaviour according to the volume of the food supply. Independently of the size of the reward, the forager shows many exploratory displays during the first visit to the source, and contrary to most ants, it never lays a trail during its first return to the nest. Visual cues remain mainly used for individual orientation; information collected during the first trips are then transmitted to nestmates thanks to temporary trail laying behaviour.

Key words: Ants, *Polyrhachis*, foraging, trail-laying, exploration.

Introduction

The social organisation of foraging in ants has been intensively studied for the last thirty years (Wilson, 1971; Hölldobler and Wilson, 1990). Ants are generally characterised by only one foraging strategy, but in fact some species use several. For example, in *Paraponera clavata*, different volumes of a nectar reward stimulate individual foraging or the mass recruitment of nestmates (Breed et al., 1987; Fewell et al., 1992). The harvester ants *Messor capitatus*, *M. struc-*

tor and *M. rufitarsis* lay a trail only when the seeds are aggregated and forage individually when the seeds are dispersed over a large area (Hahn and Maschwitz, 1985; Baroni Urbani, 1987). The strategy of predation in several species of Ponerinae also depends on the prey encountered, such as *Pachycondyla* spp. (individual foraging and tandem-running; Hölldobler and Traniello, 1980; Agbogba, 1984; Traniello and Hölldobler, 1984), *P. laevigata* (tandem-running and mass recruitment; Hölldobler and Traniello, 1980), *Paraponera clavata* (individual predation, tandem-running and mass recruitment; Breed and Bennett, 1985; Breed and Harrison, 1987), or *Ectatomma ruidum* (individual foraging, co-operative and group recruitment; Levings and Franks, 1982; Lachaud et al., 1984; Schatz et al., 1996a, b).

Only a few foraging strategies are well known in tree-dwelling ants; for example, *Oecophylla longinoda* uses five different recruitment systems (recruitment to food, to a new terrain, emigration, short- and long-range recruitment to enemies for territorial defence) (Hölldobler and Wilson, 1978). *Polyrhachis laboriosa* (F. Smith) is a non-dominant arboreal ant of the African tropical forest. The foragers individually exploit the extrafloral nectaries of different plants. In the same way, they individually exploit homopterans for their honeydew, which are generally found in areas exploited by other species of ants; they also search individually for small prey and insect corpses (Dejean et al., 1994). Nevertheless, numerous observations in the field and in the laboratory showed that some ants were also depositing from time to time abdominal marks on the substrate. Preliminary experiments showed that scouts of *P. laboriosa* use a second foraging strategy by recruiting nestmates to large insect prey and to large sugary sources (Dejean et al., 1994; Mercier, 1997).

In order to determine what are the different mechanisms involved in the choice of individual or collective foraging strategies in this species, we decided to study individual

behaviour of workers under different foraging conditions. We supposed that individual behaviour of the first forager (exploratory or recruiting behaviour, motivation of the forager) would be affected by the kind of reward it encountered. So laboratory experiments were performed and were completed with field experiments showing the initiation of recruitment on a large food supply.

Materials and methods

Three colonies of *P. laboriosa* were collected in Cameroon (Kala, Ebodjie, Ndupé). Each of them contained 300 to 500 workers and brood and were queenless, which corresponds to the most frequent structure of a nest in nature (Mercier, 1997). They were reared under laboratory conditions ($T^{\circ}\text{C} = 25 \pm 2$; humidity rate = 65–85%; photoperiod = 12 hours), in plaster nests with five chambers. Each nest was connected to a foraging arena (arena A; $20 \times 15 \times 8$ cm) by a plastic tube. Outside of experimental periods, the colonies were fed with cricket larvae, water and a mixture of apple, honey and nectar (a preparation for hummingbirds).

An experimental set-up was used to study the foraging behaviour of individuals towards a reward of sucrose: the colony tested was starved during seven days (preliminary experiments showed that this was the optimal period for eliciting foraging behaviour); on the eighth day, arena A was connected to a second foraging arena (arena B; 150×50 cm) with a wood bridge covered by filter paper ($60 \times 3 \times 20$ cm) (Fig. 1). Because *P. laboriosa* generally forages individually, we decided to study how individuals modify their behaviour over time and when confronted with different-sized rewards. For that reason, an over-turned film-box was placed at the base of the bridge in arena A and covered with silicon, so that the workers could not climb on it. This mechanism kept the workers from climbing over the box and exploring arena B. It allowed us to manually facilitate the passage over the bridge of only one worker at a time, and to study its behaviour during ten successive visits to the source during the same test. Each worker tested was previously marked with a coloured-paint droplet on the thorax.

A sucrose solution 0.1 M was placed at the centre of arena B, 10 cm away from the bridge, on the back of an overturned plastic-box (\varnothing : 4 cm). Rewards were given in increasing quantities under four different experimental conditions.

- 8 μl : the worker absorbs the entire sucrose droplet, but its crop is not full (intersegmental membranes are not visible).
- 25 μl , 125 μl , 250 μl : the worker cannot absorb all of the sucrose; its crop is full and a part of the droplet is still present in

arena B when it returns to the nest (intersegmental membranes are visible).

For each kind of reward, five different workers per colony were individually tested and three replicates were done (each ant was tested under only one condition; 4 rewards \times 5 workers \times 3 replicates = 60 workers tested). Two videotape recorders were used, the first one recording an area (50×50 cm) in the middle of arena B with the sugary source, the second one recording the entrance to the nest (the plastic tube and the two first chambers of the nest).

At the reward site, we recorded the number of cases of food absorption or the number of feeding attempts when the 8 μl source was exhausted and the number of circles made around the site).

We noted the duration of the forager's trip between the basis of bridge and the site; whether the trajectory was linear or sinuous, and the number of trail marks deposited on the bridge (Fig. 1, $n^{\circ}3$). The length of time needed for the forager to return to the nest is defined as the time spent between the last departure of the ant from the supply and its arrival to the base of the bridge (Fig. 1, trip between 1 and 2). The trail-laying behaviour of *P. laboriosa* can be distinguished by a spotted lowering of the tip of the gaster (placed vertically) to the ground. When touching the ground, the recruiter stops briefly and it is supposed that it deposits pheromonal substances.

In the nest, we measured the distance of the forager's progression, and the number of nestmates it solicited.

In all situations, the reward was replaced between each visit of the worker, so that the ant always found the same stimulus. The experiments started when the ant discovered the reward.

Field experiments were also performed with three other colonies installed in three different mango trees. We placed a food supply (a mixture of honey, sugar and water) at the periphery of the foliage and in contact with the leaves (two meters away from the nest). Then we observed how the first forager initiated the recruitment of other nestmates to the food supply.

Comparisons between the different experimental conditions were conducted using ANOVA and post-hoc Newman-Keuls tests, and discriminant analysis (STATISTICA[®] software).

Results

The main hypothesis of this work is that the first forager could use individual or collective foraging strategy as a function of the size of the reward it encountered. Therefore, it may explore, move, lay a trail and recruit more or less as a function of its motivation.

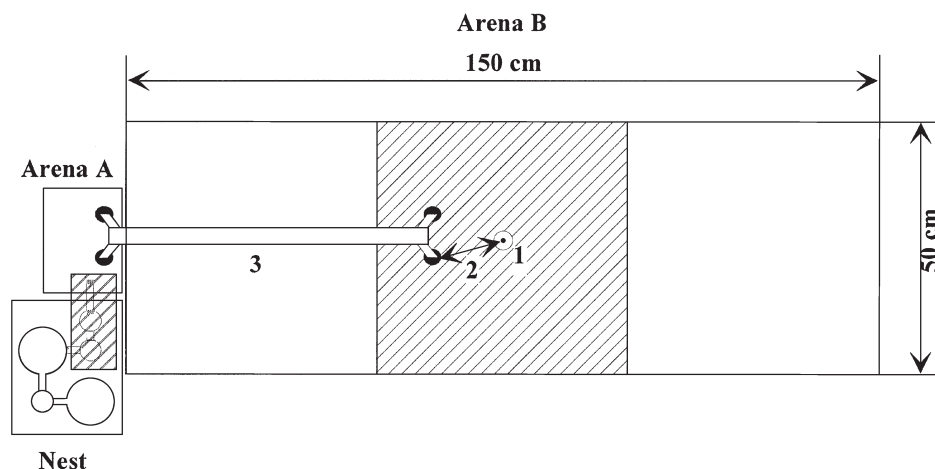


Figure 1. (1) Experimental set up used for the study of behavioural modification of the foragers of *P. laboriosa* as a function of the volume of the source. Areas in grey were filmed. 1: sucrose reward 0.1 M placed on the back of an overturned plastic-box. (2) we measured the time spent in covering the distance between the base of the bridge and the reward. (3) wood-bridge with a mechanism keeping the workers from climbing from arena A to the bridge

Laboratory experiments

The ANOVA analysis did not indicate statistical differences between the different colonies tested under the same experimental laboratory conditions, so we were able to pool the data for the three colonies.

Discriminant analysis according to the size of the supply was performed on all the behavioural items. The 8 µl supply was clearly separated from the three other rewards, and the 25 µl supply was intermediary, but of the same type as the two larger ones (Fig. 2). Among the five variables studied, three of them were significantly discriminant (food absorption or feeding attempts; circles around the supply; total number of spots laid by the forager on the bridge; $p < 0.000$). The first discriminant axis represents 93% of the variation, and is mainly correlated to the marking behaviour (coef. of corr. = 0.8).

Modification of behavioural displays upon and around the reward

When the forager was on the food site, it always fed several times before returning to the nest. When the smallest reward (8 µl) was totally absorbed, the forager attempted to feed again numerous times but did not succeed. Once it depleted the food supply, the forager moved around the site, brought its antennae forward and explored the substrate. Feeding attempts and the exploratory displays were less numerous the larger the rewards (Table 1).

Modification of behavioural displays during movement

The first trip from the nest to the source was never taken into account, because the ant did not yet know that there was a food supply.

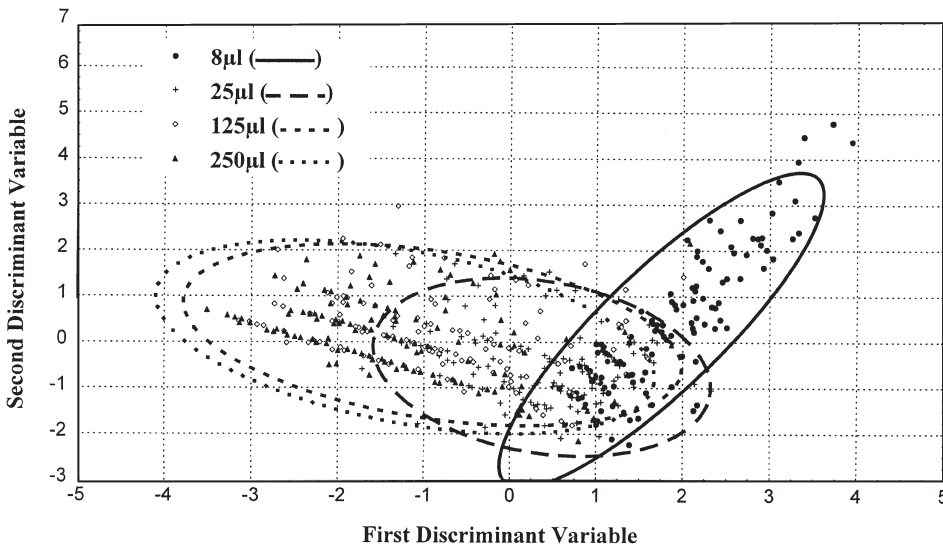


Figure 2. Discriminant analysis showing the effect of the volume of the reward on the behaviour of *P. laboriosa*. Criteria taken into account: duration of the trips; number of feeding attempts or food ingestion; number of circles around the supply; number of marks on the bridge. The measures for each kind of supply are surrounded by the confidence ellipse ($p < 0.05$). The first axis represents 93% of the variation, and is mainly correlated to marking behaviour

Table 1. Modification of the behaviour of individual foragers as a function of the volume of the source; Means and medianes with different letters are significantly different ($p < 0.05$)

Volume of the source (sucrose 0.1 M)	8 µl	25 µl	125 µl	250 µl
Number of feeding attempts* or food ingestions** (Mean ± SD)	4.97* ± 3.32 (a)	1.99** ± 1.56 (b)	1.79** ± 1.57 (b, c)	1.38** ± 1.54 (c)
Number of circles around the source (Mean ± SD)	3.12 ± 2.23 (a)	1.99 ± 1.59 (b)	1.05 ± 1.19 (c)	0.67 ± 0.82 (d)
Duration of course Bridge-Source (s) mediane (quartiles)	27.5 (9/69) (a)	16.5 (6/54) (a)	8 (5/20.5) (b)	5 (4/7.5) (b)
Duration of course Source-Bridge (s) mediane (quartiles)	552.5 (236/844.5) (a)	204.5 (78/622) (b)	86 (34/328.5) (c)	60 (23/245.5) (c)

During all the experiments, the mean duration of the trip was always shorter from the bridge to the site (5 to 27.5 s) than from the site to the bridge (60 to 552.5 s) (Table 1). The mean time for covering this distance was shorter as the size of the supply increased. The trajectory of the forager was quite linear when going to the site, except for the first trip to the site taken into account (i.e., the second visit to the site), during which exploratory displays were numerous. The trajectory was more or less sinuous when returning to the nest.

Trail-laying behaviour was very infrequent when the forager exploited a small-sized reward (8 μ l: 0.3 ± 0.6 marks/passage over the bridge) and was significantly higher as a function of the volume of the reward (Fig. 3).

Whatever the reward being used, the forager always returned to the nest the first time without laying a trail. With large-sized rewards (125 μ l and 250 μ l), the average number of marks over the bridge reached its peak between the fifth and the sixth visit of the forager to the site, then decreased slightly from 37.9 ± 3.8 to 16.9 ± 1.6 (250 μ l) and from 34.8

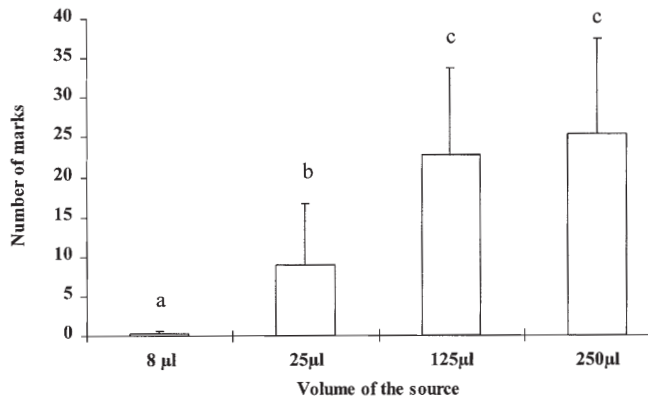


Figure 3. Modification of trail-laying behaviour over the bridge as a function of the volume of the reward (means \pm sd; $n = 15$). Bars with different letters are significantly different ($p < 0.05$)

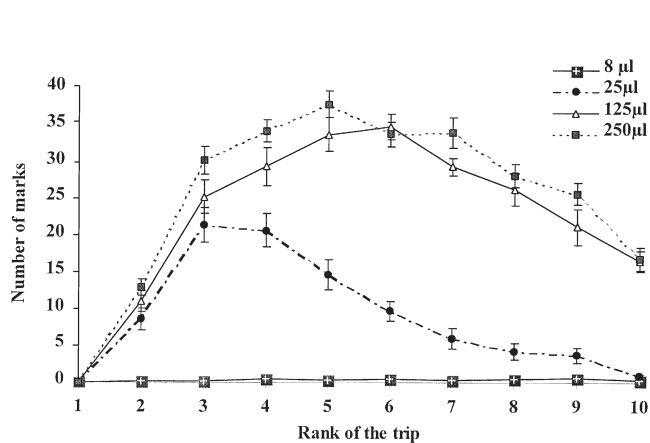


Figure 4. Modification of trail-laying behaviour over the bridge as a function of rank of the trip, for the different rewards (means \pm sd; $n = 15$)

± 3.7 to 16.5 ± 2.4 (125 μ l). Marking behaviour was lower with the intermediary reward (25 μ l) (Fig. 4).

Modification of behavioural displays inside the nest

When it returned to its nest, the forager entered more or less deeply into the chambers. This progression inside the nest was significantly higher with large-sized rewards, increasing from 5.1 ± 2 to 11.8 ± 2 cm (Fig. 5).

During the same time, the forager solicited some nestmates, the frequency of solicitation also increasing with the food supply from 1.8 ± 1 to 8.4 ± 1.6 (Fig. 5). The forager also engaged trophallaxis with one to three nestmates. Except for the exploitation of the 8 μ l droplet, the forager attempted to recruit nestmates by performing an invitation behaviour: it immobilised itself in front of a nestmate, opened its mandibles, and wagged its antennae. Nevertheless, the flow of comings and goings of nestmates (calculated from the entrance of the forager into the nest to 5 min after it left) did not vary significantly during the limited observation time in the laboratory.

Field experiments

When the first forager discovered the food supply, it fed on it. It never laid a trail during the first trip nor others until it succeeded in returning to the source without hesitation. A long time (more than five hours) and more than twenty visits of the first forager to the source were needed before the first recruited nestmates were observed on a large food supply 2 m away (Mercier, 1997). They progressively left the nest and stayed in the vicinity of the entrance. They became more and more excited each time they encountered the recruiting ant, and tried progressively to follow it to the source. Several groups of 3–6 nestmates followed the trail and arrived at the source. No more

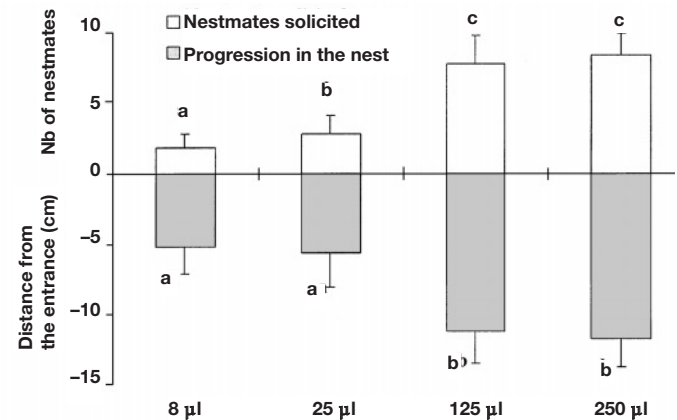


Figure 5. Modification of the behaviour of the forager inside the nest as a function of the volume of the supply (means \pm sd; $n = 15$). Bars with different letters are significantly different ($p < 0.05$)

than 35 workers were finally recruited. This group recruitment was also observed spontaneously on various occasions.

Discussion

Flexibility between individual and collective orientation during foraging has already been described in ants (Fourcassié and Beugnon, 1988; Traniello, 1989; review in Hölldobler and Wilson, 1990; Quinet and Pasteels, 1991, 1996; Fewell et al., 1992). In *P. laboriosa*, individual or group recruitment foraging strategies can be used by the first forager. In our study, small-sized rewards elicited important exploratory behaviour from the forager and trail-laying behaviour was absent. The reward being entirely absorbed before the crop of the forager was full, the worker spent a long time exploring around the site and searching for more food. In nature, small-sized rewards such as extrafloral nectaries are multiple and fairly permanent and since each of them is exploitable by only one ant of the size of *P. laboriosa* at a time, recruiting nestmates is not necessary. Exploratory displays increase the probability for the forager to find another nectary beside the first one. Indeed, they provide for the best scattering of foragers in a very complex and three dimensioned environment (the tree), in which there are many small sources of food. The way back to the nest was long when foraging on small-sized sources, because the forager was always searching for another site. But we observed that it became shorter as a function of the rank of the visit, according to the rules of navigation established by Dejean and Benhamou (1993).

In contrast, when the forager discovered a large-sized reward (a reward of at least 125 μ l), it globally performed less exploratory displays and more trail-laying behaviour. In fact, its behaviour changed over the successive visits to the site. During the first visit to a large-sized reward, the forager performed as much exploration as during the first visit to a small-sized one. No trail-laying behaviour occurred during the first return trip to the nest. This behaviour occurred only occasionally during the second trip to the site. But the ant did not find the reward immediately and moved sinuously. After the second visit to the site, the worker reinforced the trail, moved quickly and in a straight line between the site and the bridge, without exploring around the sucrose solution. The time spent returning to the nest was shorter as a function of the visit. Such a behavioural modification was already observed in other species of different genera, as a function of the characteristics of the food supply (volume, quality, concentration, density or distance) (review in Hölldobler and Wilson, 1990; Beckers et al., 1989). Two recent studies have shown that the strategy used by *Paraponera clavata* is influenced by the time spent in transit between the reward and the nest (Breed et al., 1996a, b). We were not concerned with the giving-up time variations of *P. laboriosa*, but the variation of the number of circles and of the time spent returning to the nest let us suppose that the forager spent less time on the largest food sources.

The modification of trail-laying behaviour observed in *P. laboriosa* during laboratory experiments was confirmed

with field observations. When large sources of food are found, for example a fallen, ripened fruit on a branch or on the ground, the discoverer returns to the nest and recruits nestmates, but does not lay a trail when returning to the nest for the first time (Mercier, 1997). The emergence of trail-laying behaviour may then be correlated with the persistence of the reward at the end of the visit. Furthermore, the modification of trail-laying behaviour during the experiments performed with the two large-sized rewards (125 and 250 μ l) and the intermediary reward (25 μ l) may imply that the forager differentiates between small and large volumes.

In *Formica schaufussi*, the foraging strategy used is related to the characteristics of the reward encountered by the forager during the previous trip (Fourcassié and Traniello, 1993, 1994). In *P. laboriosa*, the fact that during the first return to the nest, no trail-laying occurred and the time allotted for exploration was long, seems to indicate that the forager primarily orientated itself with visual cues and memorised the path before recruiting nestmates. Under natural conditions, the first forager moved to the right general direction of the food without laying a trail, but often took a wrong path and turned back. The foraging strategy seems to be chosen by the first forager as a function of the information collected during the early visits to the supply, the path being visually memorised before the forager lays a trail. Trail laying behaviour occurred until ten to twenty nestmates were recruited to the reward. Despite of the complexity of the environment, trail laying behaviour was not used extensively. The trail was useful only during the first trips of the recruited workers, until they memorised themselves the path to go to the food and return to the nest. They laid themselves another trail only when they did not succeed in following the first trail and were lost.

Dejean et al. (1994) in their study of predation in *P. laboriosa*, also observed a modification of the recruitment strategy according to the size of the prey. Hunters captured small prey individually but recruited nestmates to large prey; the prey was cut up in the field and pieces were individually carried back to the nest. Nevertheless, the authors did not provide any information about the moment when the recruiter laid a trail and when the recruited ants arrived at the prey.

The invitation display performed inside the nest is similar to the invitation behaviour observed in many species and particularly in *Camponotus socius* (Hölldobler, 1971). The number of solicited nestmates is also regulated by the volume of the reward exploited and may be related to the motivation of the forager.

In species which forage individually, such as the desert ant *Cataglyphis*, the solitary foragers are guided by sun-compass, the orientation and location of bushes and other landmarks, tend to persist in one or a few directions for their lifetime, and to exploit less scattered food sources (Harkness and Wehner, 1977). Nevertheless, *Cataglyphis cursor* does not recruit any nestmates to a food source (Lenoir et al., 1990). In *P. laboriosa*, vision may play an important role in the orientation of solitary foragers towards food sources, and in the memorisation of the path between large food sources and the nest. In this case, visual cues would be memorised first;

then, the recruiter would lay a trail only to recruit nestmates to the site. In such a foraging strategy, we can hypothesise that temporary trail laying behaviour plays the same role as waggle dance in bees: it permits the transfer of individual information to other nestmates, visual cues remaining mainly used for individual orientation. Therefore, there is no need for trail laying behaviour to be extensive, whatever the complexity of the environment may be.

Acknowledgements

This research was financed by a Campus grant (108 CD 90) of the French Ministry of Cooperation, entitled "Impact of tree inhabiting ants on economically important tropical trees". We thank A. Dejean, who sent us all the colonies of *P. laboriosa* from Cameroon.

References

- Agbogba, C., 1984. Observations sur le comportement de marche en tandem chez deux espèces de fourmis ponérines: *Mesoponera caffraria* (Smith) et *Hypoponera* sp. (Hymenoptera: Formicidae). *Insectes soc.* 31: 264–276.
- Baroni Urbani, C., 1987. Comparative feeding strategies in two harvesting ants. In: *Chemistry and Biology of Social Insects* (J. Eder and H. Rembold, Eds.), J. Peperny, Munich, pp. 509–510.
- Beckers, R., S. Goss, J.L. Deneubourg and J.M. Pasteels, 1989. Colony size communication and ant foraging strategy. *Psyche* 96: 239–356.
- Bolton, B., 1973. The ant genus *Polyrhachis* F. Smith in the Ethiopian region (Hymenoptera: Formicidae). *Bull. Br. Mus. Nat. Hist. Ent.* 28: 283–369.
- Breed, M.D. and B. Bennett, 1985. Mass recruitment to nectar sources in *Paraponera clavata*: a field study. *Insectes soc.* 32: 198–208.
- Breed, M.D. and J.M. Harrison, 1987. Individually discriminable recruitment trails in a ponerine ant. *Insectes soc.* 34: 222–226.
- Breed, M.D., R.M. Bowden, M.F. Garry and A.L. Weicker, 1996a. Giving-up time variation in response to differences in nectar volume and concentration in the giant tropical ant, *Paraponera clavata* (Hymenoptera: Formicidae). *J. Insect Behav.* 9: 659–672.
- Breed, M.D., J.H. Fewell, A.J. Moore and K.R. Williams, 1987. Graded recruitment in a ponerine ant. *Behav. Ecol. Sociobiol.* 20: 407–411.
- Breed, M.D., C. Stierstorfer, E.D. Furness, J.M. Jeral and J.H. Fewell, 1996b. Individual constancy of local search strategies in the giant tropical ant, *Paraponera clavata* (Hymenoptera: Formicidae). *J. Insect Behav.* 9: 673–682.
- Dejean, A. and S. Benhamou, 1993. Orientation and foraging movements in a patchy environment by the ant *Serrastruma lujae* (Formicidae, Myrmicinae). *Behav. Proc.* 30: 233–243.
- Dejean, A., A. Lenoir and E.J. Godzinska, 1994. The hunting behavior of *Polyrhachis laboriosa*, a non-dominant arboreal ant of the African equatorial forest (Hymenoptera: Formicidae, Formicinae). *Sociobiology* 23: 293–313.
- Fewell, J.H., J.F. Harrison, T.M. Stiller and M.D. Breed, 1992. Distance effects on resource profitability and recruitment in the giant tropical ant, *Paraponera clavata*. *Oecologia* 92: 542–547.
- Fourcassié, V. and G. Beugnon, 1988. How do red wood ants orient during diurnal and nocturnal foraging in a three dimensional system? I. Laboratory experiments. *Insectes soc.* 35: 92–105.
- Fourcassié, V. and J.F.A. Traniello, 1993. Effects on food-searching behavior in the ant *Formica schaufussi* (Hymenoptera: Formicidae): response of naive foragers to protein and carbohydrate food. *Anim. Behav.* 47: 287–299.
- Fourcassié, V. and J.F.A. Traniello, 1994. Food-searching behavior in the ant *Formica schaufussi* (Hymenoptera: Formicidae): response of naive foragers to protein and carbohydrate food. *Anim. Behav.* 48: 69–79.
- Hahn, M. and U. Maschwitz, 1985. Foraging strategies and recruitment behaviour in the European harvester ant *Messor rufitarsis* (F.). *Oecologia* 68: 45–51.
- Harkness, R.D. and R. Wehner, 1977. *Cataglyphis*. *Endeavour* 1: 115–121.
- Hölldobler, B. 1971. Recruitment behavior in *Camponotus socius* (Hymenoptera: Formicidae). *Z. Vergl. Physiol.* 75: 123–142.
- Hölldobler, B. and J.F.A. Traniello, 1980. Tandem running pheromone in ponerine ants. *Naturwissenschaften* 67: 360.
- Hölldobler, B. and E.O. Wilson, 1978. The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 3: 19–60.
- Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. Harvard University Press, Cambridge, 732 pp.
- Lachaud, J.P., D. Fresneau and J. Garcia-Perez, 1984. Etude des stratégies d'approvisionnement chez trois espèces de fourmis ponérines (Hymenoptera: Formicidae). *Fol. Entomol. Mex.* 61: 159–177.
- Lenoir, A., E. Nowbahari, L. Quérard, N. Pondicq and C. Delalande, 1990. Habitat exploitation and intercolonial relationships in the ant *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Acta Oecol.* 11: 3–18.
- Levings, S.C. and N.R. Franks, 1982. Patterns of nest dispersion in a tropical ground community. *Ecology* 63: 338–344.
- Mercier, J.-L., 1997. Les communications sociales chez la fourmi *Polyrhachis laboriosa* (Hymenoptera: Formicidae). Thesis of University Paris XIII. 252 pp.
- Quinet, Y. and J.M. Pasteels, 1991. Spatiotemporal evolution of the trail network in *Lasius fuliginosus* (Hymenoptera: Formicidae). *Belg. J. Zool.* 43: 55–72.
- Quinet, Y. and J.M. Pasteels, 1996. Spatial specialization of the foragers and foraging strategy in *Lasius fuliginosus* (Latreille) (Hymenoptera: Formicidae). *Insectes soc.* 43: 333–346.
- Schatz, B., J.P. Lachaud and G. Beugnon, 1996a. Flexibilité du comportement de prédation en fonction du poids des proies chez la fourmi *Ectatomma ruidum* Roger (Hymenoptera: Formicidae, Ponerinae). *Actes Coll. Insectes soc.* 10: 47–57.
- Schatz, B., J.P. Lachaud and G. Beugnon, 1996b. Polyethism within hunters of the ponerine ant, *Ectatomma ruidum* Roger (Hymenoptera: Formicidae). *Insectes soc.* 43: 111–118.
- Traniello, J.F.A., 1989. Chemical trail systems, orientation and territorial interactions in the ant *Lasius neoniger*. *J. Insect Behav.* 2: 339–354.
- Traniello, J.F.A. and B. Hölldobler, 1984. Chemical communication during tandem running in *Pachycondyla obscuricornis* (Hymenoptera: Formicidae). *J. Chem. Ecol.* 10: 783–794.
- Wilson, E.O., 1971. *The Insects Societies*. Harvard University Press, Cambridge, 548 pp.