Spatial Fidelity and Individual Foraging Specializations in the Neotropical Ponerine Ant, *Ectatomma ruidum* Roger (Hymenoptera, Formicidae)

by

Bertrand Schatz[1], Jean-Paul Lachaud[1,2,3] & Guy Beugnon[1]

ABSTRACT

In the Neotropical ponerine ant *Ectatomma ruidum*, workers involved in outside activities specialize into five behavioral categories which may be defined both on the basis of their fidelity to a given foraging site and according to their individual specialization in choice of food items or to the behavioral tasks they performed. We distinguished: on one hand hunters, honey-collecting workers and unspecialized intermediates between these two groups, and on the other hand nest-maintenance workers and patrollers clustered as "non-foragers". Moreover, among both hunters and honey-collectors, two different subsets of individuals can be segregated according to their rate of activity: "specialists" and "elite-specialists". Elitism (*sensu* Oster and Wilson 1978) and behavioral specialization are two different phenomena which can be invoked to explain the performances of an individual.

In laboratory conditions, and apart from their specialization in choice of food items, honey-collecting workers show a high spatial fidelity and use visual cues (a cross, a circle or a triangle) to locate the site on which they specialize. The adaptive value of the cognitive capacities linked to spatial fidelity are discussed according to the natural variability in local availability of certain food type.

INTRODUCTION

As a fundamental component of colony organization in social insects, division of labor has been one of the most studied phenomena in ants (Hölldobler and Wilson 1990) and within-caste specializations such as those involved in foraging appear as the highest degree of polyethism (Oster and Wilson 1978; Rissing 1981). Individual specializations in foraging tasks, however, are poorly investigated and have been reported only in a few species. Foragers of *Formica polyctena* specialize in

[1]Laboratoire d'Ethologie et Psychologie Animale, URA-CNRS 1837, Université Paul-Sabatier, F-31062 Toulouse cedex, France.
[2]El Colegio de la Frontera Sur (C.I.E.S.), Apdo Postal 36, 30700 Tapachula, Chiapas, México.
[3]To whom correspondence should be addressed

collecting primarily either honeydew, prey or nest materials (Horstmann 1973), *Pogonomyrmex rugosus*, *P. occidentalis* and *Messor (= Veromessor) pergandei* in selecting only certain seed species (Rissing 1981; Fewell and Harrison 1991), *Acromyrmex octospinosus* in showing plant preference (Therrien 1988), and *Aphaenogaster subterranea* (Agbogba 1982) or *Formica schaufussi* (Traniello 1988) in collecting either live insects or honey. In the termite hunting ponerine ant *Pachycondyla caffraria*, the only ponerine ant studied in this respect until now, an additional subdivision between "stingers" and "transporters" exists within the hunter category (Agbogba and Howse 1992).

In another ponerine ant, *Ectatomma ruidum*, food source fidelity on extrafloral nectaries has been reported (Lachaud *et al.* 1984; Passera *et al.* 1994) and our field observations (JPL, unpublished data) suggest a specialization of the foragers of this species either on carbohydrate or protein food sources. Taking this previous work as a basis, we studied, under laboratory conditions, the individual foraging specializations in choice of food items among workers of *E. ruidum* and their capacity to use visual cues related to food location as orienting cues.

Previous studies have also shown (Lachaud 1985; Pratt 1989; Breed *et al.* 1990) that when workers discover a food source, in most instances (up to 75% of the cases) the large increases of activity rates during the subsequent phase are due primarily to the response of one or two foragers. Their activity rate increases dramatically, the response consisting of shuttling repeatedly between the food source and the nest. As reported for some other ant species (Combes 1935, 1937; Fewell 1988), these observations suggest the existence of a difference in the individual rate of activity, with some individuals much more active, a phenomenon termed "elitism" by Oster and Wilson (1978). In attempting to analyze both the existence among foraging workers of *E. ruidum* of such a phenomenon and the relationship between elitism and behavioral specialization, our results were also analyzed according to the rate of activity of each worker.

MATERIALS AND METHODS

Three queen right colonies of the common Neotropical ponerine ant *Ectatomma ruidum* Roger, containing 21, 61 and 101 workers respectively, were maintained in plaster nests under controlled conditions (temperature at 25±1°C; 60±5% humidity; 12:12 hrs light/dark photoperiod starting at 08:00 hrs).

Each nest was connected with plastic tubes to a box (diameter = 10 cm) containing live crickets as a source of protein, and to the center of an arena (diameter = 30 cm) from which foragers had access through

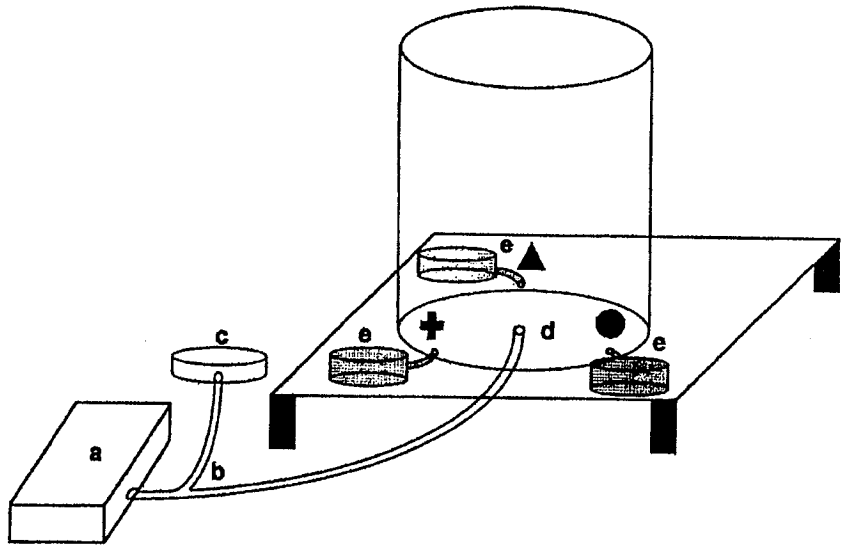

Fig. 1. Experimental set-up. (a): plaster nest; (b): plastic tubes; (c): cricket box (Ø = 10 cm); (d): center of the arena (Ø = 30 cm); (e): honey sources placed 120° apart at the periphery of the arena. The location of the entrance of each tube connected with a honey site is indicated by a specific visual landmark (a triangle, a cross and a circle) placed above the entrance of each corresponding tube on the inner wall of the arena.

plastic tubes to three different honey sites placed 120° apart at the periphery of the arena (Fig. 1). The location of each honey site was indicated by a specific visual landmark (a triangle, a cross and a circle) placed above the entrance of each corresponding tube on the inner wall of the arena.

During preliminary observations, all workers performing any sort of external activities (13, 26 and 39 workers respectively for the three colonies, i.e. 61.9%, 42.6% and 38.6% of the colony population respectively) were individually marked with enamel paint on their thorax and gaster. The three colonies were familiarized with the experimental setup for 2.5 months, during which ants were free to enter any site at any time between 08:00 and 17:30 hrs corresponding to the range of diurnal activity of this species in laboratory conditions (Schatz *et al.* 1993). During experiments, individual visits in each of the five potential foraging sites (the cricket box, the arena and the three honey sites) and all entries or exits were scanned between 08:00 and 17:30 hrs, every 15 min during 4 days (n=152 scans for each colony). For each worker displaying external activities, we recorded: identity, foraging site visited, and timing of each foraging trip. As it was expected in this

species (Lachaud 1985), the workers forage individually and no mass recruitment nor trail laying was observed during the search for food. Nevertheless, because it has been shown that *E. ruidum* workers sometimes can lay chemical trails when searching for carbohydrates (Pratt 1989), the floor of the arena was cleaned with alcohol before each of the four days of observation to eliminate any possible chemical directional information.

A "fidelity coefficient" (FC), defined as the ratio between number of visits recorded for an individual at a given visited site and total number of trips of this individual during the observation period, was calculated for each individual. When considering the five potential foraging sites (cricket box, arena and each of the three honey sites), all workers presenting a fidelity coefficient for a given site with a value FC≥0.50 (i.e. which were visiting this site in more than 50% of all their trips, with a minimum of two trips in the same site), were considered as true to this site. When considering only the three types of foraging sites (cricket box, arena, and honey sites), or each of the three honey sites, the fidelity level value was fixed at FC≥0.70. All individuals presenting similar fidelity coefficients for the most visited site (FC≥0.50 or FC≥0.70 according to the number of foraging sites considered) were clustered and treated as a specific behavioral category of workers.

RESULTS

Task specialization

Only 68 of the 78 initially marked workers recorded outside the nest were active during the 4-day observation period: 4 workers from the medium colony and 6 from the biggest one were never seen outside the nest during this period. Due to the very low sample size for specialist workers in each colony, data for the three colonies were pooled.

According to the differences noted (Fig. 2) between the fidelity coefficients corresponding to the frequenting of the three different types of foraging sites (cricket box, honey sources, arena), a very strong differentiation into four behavioral categories appeared among the workers: hunters, honey-collectors, unspecialized intermediates, and non-foragers, the differences between the categories being highly significant (X^2 test>>24, $p<0.0001$).

Hunters. Of the 187 visits to the cricket site recorded for the three colonies over the 4-day observation period, 173 (92.5%) were made by 12 workers (3, 4 and 5 workers respectively for the three colonies) representing 15.4% of the forager force (n = 78). These "hunters", which presented an average fidelity to the cricket site of 0.83 ± 0.15 (median:

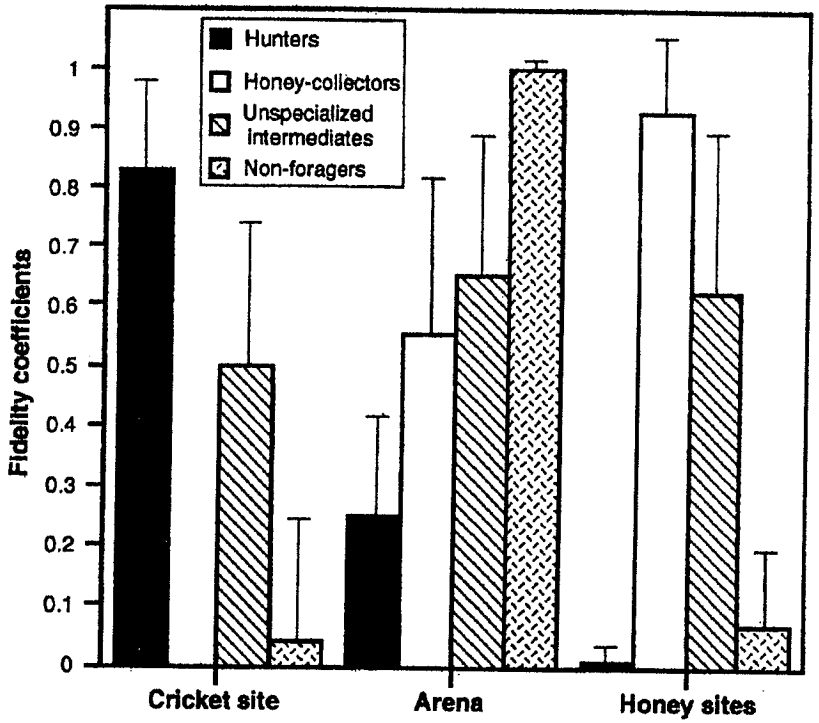

Fig. 2. Foraging site fidelity in workers of *Ectatomma ruidum* displaying outside activities. The data from the three colonies were pooled for each foraging site type (cricket site, arena or honey sites) according to the fidelity coefficients (number of records/number of trips) calculated for the site most visited by individual foragers. For other comments see text.

0.82), visited also the arena in which they displayed search behavior and were spotted only twice at a honey site but did not transport honey to the nest.

Honey-collectors. Of the 501 visits to the three honey sites recorded for the three colonies, 473 (94.4%) were performed by 24 specialized workers (4, 8 and 12 workers) representing 30.8% of the forager force. All these "honey-collectors" presented a very homogeneous high average fidelity to the honey sites of 0.93 ± 0.13 (median: 1).

The frequency of all visits to the three honey sites (associated with the cross, the circle or the triangle) was similar over the 4-day observation period (167, 171 and 163 visits respectively), indicating that there was no preference, at the colony level, for any of the three visual cues. Nevertheless, an analysis of the site fidelity at the individual level showed that the foragers distributed into four homogeneous groups

according to their fidelity (or absence of fidelity) to a given honey site: 22 workers presented an average fidelity to one of the three honey sites of 0.91±0.13 (median: 0.97) while 2 other workers presented a similar global average fidelity to the honey sites of 0.93 but maintained no fidelity to any of the three honey sites. Among the faithful workers, 7 were faithful to the honey site associated with the cross (average $FC_{honey\ site\ "cross"}$ = 0.97±0.04; median: 1), 8 to the site associated with the circle (average $FC_{honey\ site\ "circle"}$ = 0.85±0.19; median: 0.94) and 7 to the site associated with the triangle (average $FC_{honey\ site\ "triangle"}$ = 0.92±0.09; median: 0.94). This fidelity to a given visual cue appears even more dramatic when we consider the frequency of visitation rate to each honey site (ratio between number of visits to a given honey site and total number of visits to the three honey sites). Of the 448 visits recorded for the faithful workers to the honey sites, 98.9% were made to only one of the three honey sites (Fig. 3) while for the two unfaithful honey-collectors the frequency of visitation rates to the three honey sites were of 12.0, 40.0 and 48.0% respectively.

The task specialization of the honey collecting workers was extremely clear since none of them was ever spotted at the cricket site over 528 trips. Even if they visited the arena in 64.7% of their trips, this does not mean that they show any fidelity for this site since these ants must necessarily go through the arena to reach the honey sites or come back to the nest.

Unspecialized intermediates. Eight workers (1, 2 and 5 workers respectively), representing 10.3% of the forager force, were distributed into the various available sites without clear fidelity to any of the three types of foraging site ($FC_{cricket\ site}$ = 0.50±0.24; $FC_{honey\ sites}$ =0.62±0.27; FC_{arena}=0.65±0.23). In comparison with hunters and honey-collectors, they presented an homogeneous intermediate behavioral profile, all workers performing both hunting and honey-collecting activities.

Non-foragers. This heterogeneous group consists of 24 workers (5, 8 and 11 workers respectively) corresponding to 30.8% of the forager force. While representing only 25.7% of all visits recorded in the arena, they show an extreme fidelity to this site (FC_{arena} = 1±0.02; median: 1) and were spotted only rarely at cricket ($FC_{cricket\ site}$ = 0.04±0.20) or honey ($FC_{honey\ sites}$ = 0.07±0.13) sites.

On several occasions, some of these workers (n=10) were seen transporting various items (plaster, cocoon debris, prey remains) outside the nest while always returning to the nest with empty mandibles. These transports account for 94.4% of all transports (n=36) recorded for the three colonies. Most of the other individuals of this group, characterized by long and sinuous trips, showed no interest in

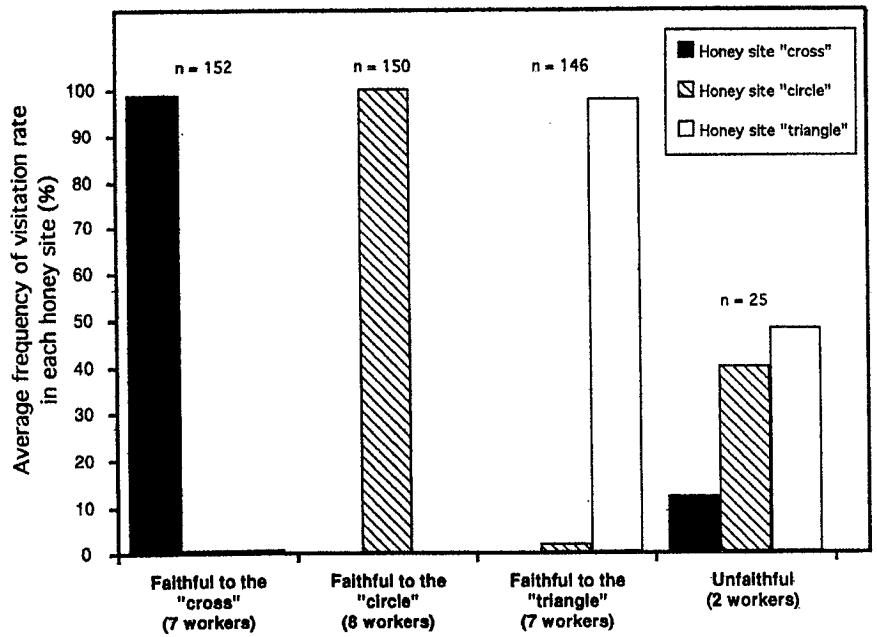

Fig. 3. Frequency of visitation rate displayed by the four categories of honey collectors to each of the three honey sites (indicated by a cross, a circle or a triangle landmark). For other comments see text.

honey or prey.

Behavioral specialization and elitism

According to the individual activity rate (estimated by the number of trips) of the workers active outside the nest, we defined (Fig. 4) a segregating level of activity corresponding to 1.5 times the average activity rate (x = 11 trips) of the 78 workers potentially active outside the nest. We thus segregated two categories of workers: those performing an activity rate lower than this segregating level of activity (1.5x = 16.5 trips), and those performing an activity rate superior (≥17 trips). For each behavioral category, and independently of the value of the fidelity coefficient associated to the site linked to the category under consideration, two subgroups of workers were considered (Fig. 4): (a) very active specialists, termed "elite-specialists" *sensu* Oster and Wilson (1978), which made more than 17 visits to the more visited site over the 4-day observation period; and (b) "specialists" which were much less active (≤11 visits). According to our criterion, no elitism was found among unspecialized workers or non-foragers.

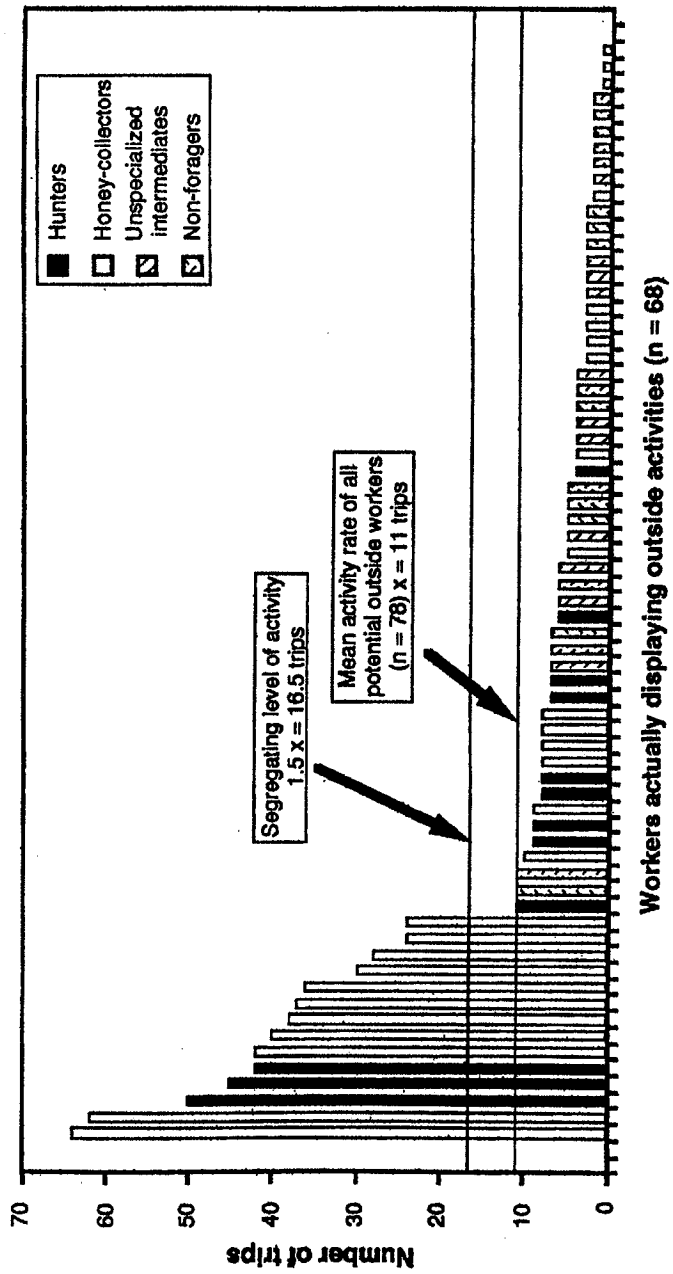

Fig. 4. Individual activity rates of the 68 workers displaying outside activities. The segregating level of activity between "elite" and other workers corresponds to 1.5 times the mean activity rate of the 78 workers potentially active outside the nest. For other comments see text.

Of the 473 visits to the three honey sites made by the 24 honey-collectors, 411 (86.9%) were performed by 11 elite-specialists and only 62 (13.1%) by 13 less active specialists. Similarly, among the hunters, 3 elite-specialists performed 119 (68.8%) of the 173 visits of this group to the cricket site while the other 9 specialists of this behavioral category performed only 54 visits (31.2%) to this food site. Nevertheless, when we compared specialists (n = 22) and elite-specialists (n = 14) according to their fidelity coefficient for the most visited food site, no significant difference was encountered between both categories (0.95±0.06 vs. 0.86 ±0.17).

DISCUSSION

We found strong evidence of the existence of behavioral specializations in *Ectatomma ruidum* foragers, not only with regard to food site fidelity but also with regard to individual specialization in choice of food items. According to their food specialization and/or degree of site fidelity, a minimum of four behavioral categories could be differentiated: hunters, honey-collectors, unspecialized intermediates and non-foragers. Nevertheless, if one considers the classification of colony activities made by Gordon (1986) and Adler and Gordon (1992), the category described in this study as "non-foragers" could, in fact, embrace two kinds of workers specialized in different tasks: "nest maintenance" for the workers mostly involved in nest material transport and performing 94.4% of this task, and "patrollers" for those characterized by long and sinuous paths (a typical pattern of search behavior, see Déjean *et al.* 1993) and showing no interest in honey or prey.

As in *Pachycondyla caffraria* (Agbogba and Howse 1992), our data suggest that colony size in *E. ruidum* is likely to affect both the total number of workers involved in activities outside the nest and the way this forager force is organized. We noted an inverse correlation between the colony size and the proportion of foragers (61.9% of the worker population for the smallest colony, 42.6% for the medium and 38.6% for the biggest one). Moreover, while some foragers of the two larger colonies (15.4% of the foragers in both cases) were never seen outside the nest during the 4-day observation period, all the foragers of the smallest colony (13 workers) were active during the same period.

Unspecialized intermediates and non-foragers are mainly characterized respectively by an absence of specialization in terms of food type or of site fidelity. By contrast, food specialization, defined as the tendency to consistently choose the same food item when others are available (Nickel and Neal 1972; Rissing 1981; Fewell and Harrison

1991), is a common and strong characteristic of the two other behavioral subcastes. Honey-collectors were indeed never spotted at the cricket site over the 528 trips they made outside the nest, and hunters were spotted at a honey site only twice over 207 trips. A similar constancy in food preference has been reported in the formicine *Formica schaufussi* (Fourcassié and Traniello 1994) and in *Pachycondyla caffraria* (Agbogba and Howse 1992), an other ponerine ant species.

The existence of two very different activity rates among individual workers of *E. ruidum* specialized in hunting or honey collecting, leading to a differentiation between "specialists" and "elite-specialists", adds a further qualitative dimension to the notion of task specialization. Such a difference in the individual rate of activity has been reported casually in few other ant species (Combes 1935, 1937; Verron 1974; Traniello 1977; Fewell 1988; Fewell and Harrison 1991) and may account for the considerable inter-individual variation in the intensity of specialization recorded during brood transport in *Tapinoma erraticum* (Meudec 1973, 1977) or during adult transport in the course of nest moving in *Formica sanguinea*, *F. fusca*, and *Camponotus sericeus* (Möglich and Hölldobler 1974, 1975). Analyzing the relation between within-caste elitism, specialization, and idiosyncrasy, Oster and Wilson (1978 p. 155) concluded that "*Division of labor has been elaborated in many species by elitism, defined as the existence of exceptionally active or entrepreneurial individuals within age-size cohorts.*", suggesting that this elitism was the prime mover of the behavioral specialization. Our data suggest a more shaded answer to this question. The most active ants in one behavioral category are neither generally elites nor the only specialists in the category under observation since, as far as their fidelity coefficient for the most visited site is concerned, no significant difference was encountered between elite-specialists and specialists. Consequently within-caste elitism and behavioral specialization appear as two different phenomena. Nevertheless, according to the model developed in *Pachycondyla* (= *Neoponera*) *apicalis* by Deneubourg *et al.* (1987), and in agreement with Oster and Wilson's (1978) conclusion, the difference in activity rate is likely to affect the mechanism of site fidelity linked with food specialization: a more rapid learning of the route from the nest to the site of previous food find leading to a stronger food site fidelity. As pointed out by Traniello (1989) and Johnson (1991), given the unpredictability of the food resource in the environment of a colony, foragers' learning abilities are closely related with foraging efficiency. In *E. ruidum*, the use of visual landmarks (Jaffé *et al.* 1990, Schatz *et al.* 1994 and this study) allows individual foragers to return to and search at the site of their prior food find, resulting in enhanced individual and colony-

wide foraging efficiency in a manner similar to "majoring" in bumblebees and honeybees (Heinrich 1976, 1979). Such a site fidelity, based on familiarity of visual or chemical cues, is well documented in the harvester ants *Pogonomyrmex* spp. (Bernstein 1975; Hölldobler 1976; De Vita 1979; Crist and MacMahon 1991a) and in few other genera like *Formica* (Rosengren 1971; Beugnon and Fourcassié 1988; Traniello 1988; Lamb and Ollason 1993), and *Cataglyphis* (Wehner 1992; Pastergue-Ruiz *et al.* 1995). In contrast to the majority of these species, with the exception of *Pogonomyrmex occidentalis* for which site fidelity was shown to vary between 3 (Crist and MacMahon 1991b) and 6 days (Fewell 1990) according to the situation, site fidelity in *E. ruidum* is relatively short, lasting a minimum of 4 (these results) to 6 days (Lachaud *et al.* 1984). The simultaneous existence of short-term site fidelity (or lack of site fidelity in some cases) and long-term food type preference suggests an adaptive mechanism in the choice of food site based on an interaction between individual foraging history and the variability in local availability of certain food type. This hypothesis is supported by field observations made on *E. ruidum* in the island of Guadeloupe (West Indies), showing a relationship between individual temporal learning and food site fidelity (Passera *et al.* 1994). Workers visiting extrafloral nectaries of the orchid *Spathoglotis plicata* showed site fidelity for at least 5 days, corresponding to the period during which these flowers produced secretion (Jaffé *et al.* 1989). Such shifts in site fidelity linked to a complex and fluctuating environment have to be correlated with the capacity of *E. ruidum* workers to associate temporal and spatial changes in the daily pattern of food availability (Schatz *et al.* 1994) and to modify their rhythm of activity accordingly (Schatz *et al.* 1993). These adaptive strategies, combined with the control of time information by individual ants (Schatz *et al.* 1994) and a high spatial fidelity according to their food specialization (these results), suggest that *E. ruidum* workers are highly flexible. This flexibility appears of great adaptive value in natural conditions where sugar food sources are dispersed and mainly provided by extrafloral nectaries which produced secretion only at some specific time of the day.

ACKNOWLEDGMENT

This research was supported by grants from the "Sciences de la Cognition" (MRE), the "Cognisciences" program of the CNRS to the "Pole de Recherche en Sciences Cognitives de Toulouse" (PRESCOT) and the "Conseil Régional Midi-Pyrénées". We are grateful to R. Wehner, R.A. Johnson and V. Fourcassié for their critical reading of a previous draft of this manuscript.

REFERENCES

Adler, F.R. & D.M. Gordon 1992. Information collection and spread by networks of patrolling ants. Am. Nat. *140*: 373-400.

Agbogba, C. 1982. *Contribution à l'étude de la prédation et de l'approvisionnement de la société chez des fourmis carnivores. Analyse comparée chez des espèces d'Afrique tropicale et du midi de la France.* Thèse de Doctorat, Université Aix-Marseille, 132 pp.

Agbogba, C. & P.E. Howse 1992. Division of labour between foraging workers of the ponerine ant *Pachychondyla caffraria* (Smith) (Hymenoptera: Formicidae). Ins. Soc. *39*: 455-458.

Bernstein, R.A. 1975. Foraging strategies of ants in response to variable food density. Ecology *56*: 213-219.

Beugnon, G. & V. Fourcassié 1988. How do red wood ants orient when foraging in a three dimensional system? 1. Field experiments. Ins. Soc. *35*: 106-124.

Breed, M.D., P. Abel, T.J. Bleuze & S.E. Denton 1990. Thievery, home ranges, and nestmate recognition in *Ectatomma ruidum*. Oecologia *84*, 117-121.

Combes, M. 1935. Observations d'après lesquelles l'activité des fourmis serait le fait d'une minorité de travailleuses dans tous les groupements étudiés. Annls Sci. Nat. (Zool.) *(10) 18*: 97-102.

Combes, M. 1937. Existence probable d'une élite non différencié e d'aspect, constituant les véritables ouvrières chez les *Formica*. C. R. Acad. Sci., Paris *204*: 1674-1675.

Crist, T.O. & J.A. MacMahon 1991a. Individual foraging components of harvester ants: movement patterns and seed patch fidelity. Ins. Soc. *38*: 379-396.

Crist, T.O. & J.A. MacMahon 1991b. Foraging patterns of *Pogonomymrmex occidentalis* (Hymenoptera: Formicidae) in a shrub-steppe ecosystem: the roles of temperature, trunk trails, and seed resources. Environ. Entomol. *20*: 265-275.

Déjean, A., G. Beugnon & J.-P. Lachaud 1993. Spatial components of foraging behaviour in an African ponerine ant, *Paltothyreus tarsatus*. J. Insect Behav. *6*: 271-285.

Deneubourg, J.-L., S. Goss, J.M. Pasteels, D. Fresneau & J.-P. Lachaud 1987. Self-organization mechanisms in ant societies (II): Learning in foraging and division of labor, pp. 177-196. *In*: Pasteels J.M. & Deneubourg J.-L., Edits. *From individual to collective behavior in social insects (Experientia Suppl., Vol. 54)*. Basel: Birkhäuser Verlag.

De Vita, J. 1979. Mechanisms of interference and foraging among colonies of the harvester ant *Pogonomyrmex californicus* in the Mojave Desert. Ecology *60*: 729-737.

Fewell, J.H. 1988. Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. Behav. Ecol. Sociobiol. *22*: 401-408.

Fewell, J.H. 1990. Directional fidelity as a foraging constraint in the harvester ant, *Pogonomyrmex occidentalis*. Oecologia *82*: 45-51.

Fewell, J.H. & J.F. Harrison 1991. Flexible seed selection by individual harvester ants, *Pogonomyrmex occidentalis*. Behav. Ecol. Sociobiol. *28*: 377-384.

Fourcassié, V. & J.F.A. Traniello 1994. Food searching behaviour in the ant *Formica schaufussi* (Hymenoptera, Formicidae): response of naive foragers to protein and carbohydrate food. Anim. Behav. *48*: 69-79.

Gordon, D.M. 1986. The dynamics of the daily round of the harvester ant colony (*Pogonomyrmex barbatus*). Anim. Behav. *34*: 1402-1419.

Heinrich, B. 1976. The foraging specialization of individual bumblebees. Ecol. Monographs *46*: 105-128.

Heinrich, B. 1979. "Majoring" and "minoring" by foraging bumblebees, *Bombus vagans*: an experimental analysis. Ecology 60: 245-255.

Hölldobler, B. 1976. Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. Behav. Ecol. Sociobiol. *1*: 1-44.

Hölldobler, B. & E.O.Wilson 1990. *The ants*. Berlin: Springer-Verlag, 732 pp.

Horstmann, K. 1973. Untersuchugen zur Arbeitstalung unter der Aussendienst-arbeiterinnen der Waldameise *Formica polyctena* Foerster. Z. Tierpsychol. *32*: 532-543.

Jaffé, K., C. Pavis, G. Vansuyt & A. Kermarrec 1989. Ants visit extrafloral nectaries of the orchid *Spathoglotis plicata* Blume. Biotropica 21: 278-279.

Jaffé, K., C. Ramos, C. Lagalla & L. Parra 1990. Orientation cues used by ants. Ins. Soc. 37: 101-115.

Johnson, R.A. 1991. Learning, memory, and foraging efficiency in two species of desert seed-harvester ants. Ecology *72*: 1408-1419.

Lachaud, J.-P. 1985. Recruitment by selective activation: an archaic type of mass recruitment in a ponerine ant (*Ectatomma ruidum*). Sociobiology *11*: 133-142.

Lachaud, J.-P., D. Fresneau & J. García-Pérez 1984. Etude des stratégies d'approvisionnement chez trois espèces de fourmis Ponérines (Hymenoptera, Formicidae). Folia Entomol. Méx. *61*: 159-177.

Lamb, A.E. & J.G. Ollason 1993. Foraging wood-ants *Formica aquilonia* Yarrow (Hymenoptera: Formicidae) tend to adopt the ideal free distribution. Behav. Processes *28*: 189-198.

Meudec, M. 1973. Note sur les variations individuelles du comportement de transport du couvain chez les ouvrières de *Tapinoma erraticum* Latr. C. R. Acad. Sci., Paris (D) *277*: 357-360.

Meudec, M. 1977. Le comportement de transport du couvain lors d'une perturbation du nid chez *Tapinoma erraticum*. Rôle de l'individu. Ins. Soc. *24*: 345-352.

Möglich, M. & B. Hölldobler 1974. Social carrying behavior and division of labor during nest moving in ants. Psyche *81*: 219-236.

Möglich, M. & B. Hölldobler 1975. Communication and orientation during foraging and emigration in the ant *Formica fusca*. J. Comp. Physiol. *101*: 275-288.

Nickel, D.A. & T.M. Neal 1972. Observations of foraging behavior of southern harvester ants, *Pogonomyrmex badius*. Fla. Entomol. *55*: 65-66.

Oster, G.F. & E.O. Wilson 1978. *Caste and ecology in the social insects.* Princeton, New Jersey: Princeton University Press, 352 pp.

Passera, L., J.P. Lachaud & L. Gomel 1994. Individual food source fidelity in the neotropical ponerine ant *Ectatomma ruidum* Roger (Hymenoptera Formicidae). Ethol. Ecol. Evol. *6*: 13-21.

Pastergue-Ruiz, I., G. Beugnon & J.-P. Lachaud 1995. Can the ant *Cataglyphis cursor* encode global landmark-landmark relationships in addition to isolated landmark-goal relationships? J. Insect. Behav. *8*, 115-132.

Pratt, S., 1989. Recruitment and other communication behavior in the ponerine ant *Ectatomma ruidum.* Ethology *81*: 313-331.

Rissing, S.W. 1981. Foraging specializations of individual seed-harvester ants. Behav. Ecol. Sociobiol. *9*: 149-152.

Rosengren, R. 1971. Route fidelity, visual memory and recruitment behaviour in foraging wood ants of the genus *Formica* (Hymenoptera, Formicidae). Acta Zool. Fenn. *133*: 1-106.

Schatz, B., G. Beugnon & J.-P. Lachaud 1994. Time-place learning by an invertebrate, the ant *Ectatomma ruidum* Roger. Anim. Behav. *48*: 236-238.

Schatz, B., J.-P. Lachaud & G. Beugnon 1993. Apprentissage temporel chez la ponérine néotropicale *Ectatomma ruidum* Roger. Actes Coll. Ins. Soc. *8*: 9-15.

Therrien, P. 1988. Individual food choices by foragers from the species *Acromyrmex octospinosus* Reich the leaf-cutting ant. Mem. Entomol. Soc. Can. *146*: 123-130.

Traniello, J.F.A. 1977. Recruitment behavior, orientation, and the organization of foraging in the carpenter ant *Camponotus pennsylvanicus* DeGeer (Hymenoptera: Formicidae). Behav. Ecol. Sociobiol. *2*: 61-79.

Traniello, J.F.A. 1988. Variation in foraging behavior among workers of the ant *Formica schaufussi*: ecological correlates of search behavior and the modification of search pattern, pp. 91-112. *In*: Jeanne R.L., Edit. *Interindividual behavioral variability in social insects.* Boulder: Westview Press.

Traniello, J.F.A. 1989. Foraging strategies of ants. Annu. Rev. Entomol. *34*: 191-210.

Verron, H. 1974. Note sur l'activité locomotrice des ouvrières de *Lasius niger.* C. R. Acad. Sci., Paris (D) *285*: 419-421.

Wehner, R. 1992. Arthropods, pp. 45-144. In: Papi F., Edit. *Animal homing.* London: Chapman & Hall.