Foraging ecology and behaviour of the ponerine ant *Ectatomma opaciventre* Roger in a Brazilian savannah

M. R. PIE[1]

Departamento de Zoologia, Universidade Estadual de Campinas, 13083 970 Campinas SP, Brazil

This study provides a detailed account of the foraging behaviour of the ponerine ant *Ectatomma opaciventre* in a 'cerrado' savannah in south-east Brazil. Our observations suggest that this species has an exclusively diurnal foraging pattern. Feeding habits included both predation and scavenging, with termite workers and leaf-cutting ants as the most important food items. Contrary to all other *Ectatomma* species studied to date, no liquid food such as hemipteran honeydew or plant nectar was collected. Foragers showed clear individual foraging area fidelity. Workers of *E. opaciventre* employed a typical individual foraging strategy, i.e. there was no co-operation between foragers in the search for or retrieval of food, neither by tandem running nor by trail laying. Nest density was considerably lower than in other *Ectatomma* (0.015 nests per m²). The observed mean distance to the nearest neighbouring nest was 5.85 m, with a significant tendency toward over-dispersion. Nests were more frequently found in specific microhabitats, which may suggest active choice of nesting site by founding queens.

KEYWORDS: Cerrado, nest density, foraging behaviour, path fidelity.

Introduction

The family Formicidae is characterized by an extreme variety of diets and foraging strategies (Hölldobler and Wilson, 1990). Although many authors have attempted to assess patterns underlying this diversity (e.g. Rosengren and Sundström, 1987; Houston *et al.*, 1988; Beckers *et al.*, 1989), the development of hypotheses about ant foraging strategies is hampered by the relative scarcity of quantitative data on the foraging behaviour of the different species (Carrol and Janzen, 1973; Traniello, 1989; Tschinkel, 1991; Duncan and Crewe, 1994). Only a comparison between the different species will enable us to understand the diverse patterns of ecological adaptations to foraging (Duncan and Crewe, 1994).

Among the extant ant subfamilies, the Ponerinae is usually considered as one of

---

[1]Present address: Department of Biology, Boston University, 5 Cummington St., Boston, MA 02215, USA; e-mail: pie@bu.edu

the most primitive groups, both behaviourally and morphologically (Wheeler, 1910; Wilson, 1971; Hölldobler and Wilson, 1990). Their basal position makes their study valuable for understanding the factors that influence processes such as the evolution of feeding preferences and recruitment systems (Breed and Bennet, 1985). The genus *Ectatomma* is relatively recent in this subfamily, being composed of 14 species, all of which are endemic to South and Central America (Brown, 1958; Fresneau *et al.*, 1982; Kugler and Brown, 1982; Baroni Urbani *et al.*, 1992; Bolton, 1995). These ants are considered to be generalist predators on a variety of small arthropods and annelids, occasionally collecting extrafloral nectar and hemipteran honeydew (Fernández, 1991; Oliveira and Brandão, 1991; Del-Claro and Oliveira, 1999). An impressive variety of foraging strategies have been found in *Ectatomma.* For instance, *E. ruidum* has been recorded using strategies such as ambush predation (Schatz and Wcislo, 1999), solitary hunting, co-operative hunting and group hunting with recruitment (Schatz *et al.*, 1997), forager specialization in particular food types (Schatz *et al.*, 1995) and even cleptobiosis (Perfecto and Vandermeer, 1993). In contrast to the information available on *E. ruidum* and *E. tuberculatum* (e.g. Wheeler, 1986; Dejean and Lachaud, 1992; Valenzuela-González *et al.*, 1995), very little is known about the foraging behaviour of other *Ectatomma* species, particularly *E. opaciventre*. It is known to nest in the soil and to forage in the epigaeic layer, and is the most common *Ectatomma* species found nesting in open and dry habitats, such as savannahs (Brown, 1958; Kempf, 1972; Fernández, 1991). The worker caste in *E. opaciventre* is monomorphic, and the workers are among the largest ants in the genus (∼1.5 cm, see figure 1). Nests are relatively shallow (usually <70 cm in depth) and with a single entrance, followed by an unbranched series of chambers (Antonialli-Junior and Giannotti, 1997). Colonies are fairly small, composed of 60–120 workers (Antonialli-Junior and Giannotti, 1997). This work represents the first detailed

FIG. 1.   Forager of *Ectatomma opaciventre* preying on a termite.

study on the foraging behaviour of *E. opaciventre*. We provide a qualitative and quantitative account of the foraging biology of the species, with emphasis on the following aspects: (1) daily foraging rhythm; (2) composition and abundance of dietary items; (3) nest dispersion and location according to microhabitat; and (4) spatial foraging fidelity by foragers.

Materials and methods

The study site

Field work was carried out in the Estação Experimental de Itirapina (EEI), São Paulo State, Brazil (22°15′S, 47°49′W). According to Köppen's classification, the region of Itirapina has a *Cwa* climate, with a dry cold season from April to September and a rainy warm season from October to March (Giannotti, 1988). The vegetation at EEI corresponds to the cerrado *sensu stricto* of Goodland (1971). The vegetation at the study site was open, consisting basically of grasses and some scattered palm trees (figure 2).

Daily activity pattern and diet

During April and May 1997 we tagged 40 nests of *E. opaciventre*, which were found by presenting foragers with tuna baits and following them back to their nests. Four of these colonies (> 10 m apart) were monitored over 24 h to describe the daily foraging activity pattern. Sampling consisted of counting the number of ants entering
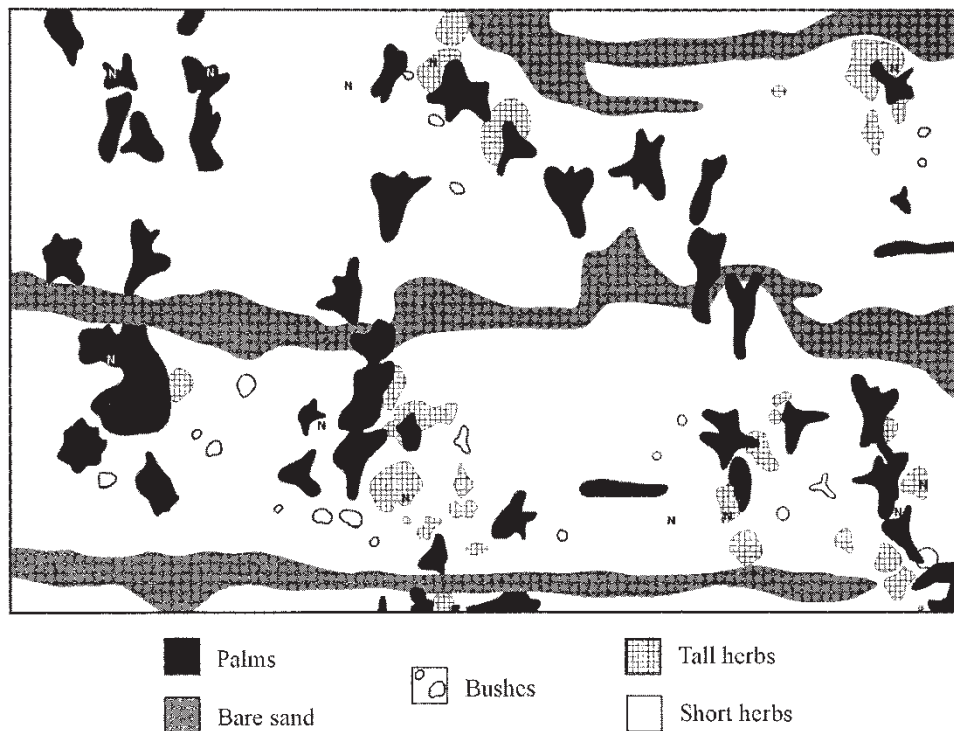

FIG. 2. General physiognomic map of the study area in the cerrado of Itirapina, south-east Brazil. Nests (N) of *Ectatomma opaciventre* and the different types of microhabitat are indicated. Categories 'palms' and 'bushes' were combined for the analyses.

and exiting the nest during 40 min at 2-h intervals. Temperature and humidity were recorded hourly. Based on knowledge about the periods of increased foraging activity, dietary items were collected from 8 to 11.30 a.m. and from 2 to 4.30 p.m., totalling 19 h and 30 min of sampling. Samples were taken by searching for workers in foraging activity and collecting the items from their mandibles. When a forager was spotted with an item between its mandibles the item was promptly collected. Unladen workers were followed for about 5 min. If during this period the forager found a food item, the ensuing interaction was recorded. Food items were kept in 70% alcohol for later identification. In the laboratory, the items were placed in a convection oven at approximately 60°C for 24 h. Dry weight was then obtained using a Mettler H51 Ar balance. The availability of the food resources in the study site was evaluated using pitfall traps. Seventeen of these traps were distributed regularly in the study site and were opened and checked on 11 and 24 July and 4 August. In order to prevent recording food items that were not available during the ant's foraging activity, the traps remained open only during the foraging period of *E. opaciventre* (i.e. from 8 a.m. to 5 p.m.).

Nest spacing and nesting site preference

A fraction of the study site (900 m²) was divided into a 1 m grid using measuring tapes. An exhaustive survey was then undertaken to map all nest entrances of *E. opaciventre*. The nest spacing pattern was analysed using the Clark and Evans' (1954) nearest-neighbour method, which provides the index R, which ranges from 0 (perfect aggregation) to 2.1491 (perfectly hexagonal dispersion). The quantity $R = 1$ indicates a random distribution. The statistical significance is then tested using the Z transformation. Since we counted only the nests inside this area, a Donnely correction was employed for the expected nearest neighbour (Krebs, 1989). Based on this grid we also constructed a physiognomic map of the area (figure 2), using the following categories: (I) short herbs (up to 15 cm tall); (II) tall herbs (up to 50 cm tall); (III) bare sand; (IV) bushes + palms. This map was then drawn on a large paper sheet, and each category was cut out from this map and weighted in order to estimate the relative area of each microenvironment. These values were then compared with the observed number of nests in each of these microenvironments in order to assess a microhabitat preference for nesting sites by *E. opaciventre*.

Foraging strategy

The study of the foraging strategy of *E. opaciventre* was based on detailed observations of two colonies. Each colony was observed for 5 days, from 8.30 to 11.30 a.m., and from 2.30 to 4.00 p.m. In each colony, every forager was marked with a distinct colour code (Enamel Paint, Testors Co., Rockford, USA), allowing their prompt identification in the field. An 8 m² grid around the nest entrance allowed the recordings of individual foraging paths. Every ant exiting the nest was followed individually for the duration of its foraging trip. As the ant walked, a numbered pin was placed on the ground along its route each 60 s. In case the ant showed any sign of disturbance caused by the observer, the data were discarded. This procedure enabled us to record the time and the length of each foraging path. Each path was then converted to a smaller grid on a paper, digitized and overlapped with the other paths.

Results

The ants foraged exclusively during the day, with two activity peaks, a larger one in the morning and a smaller peak in the afternoon (figure 3a, b). Observations throughout the 24-h study period suggest that this pattern was consistent, with very few foragers seen at midday and after 5.00 p.m. However, even during the peak hours the number of foragers did not exceed a few workers. A correlation analysis between the daily foraging rhythms of the different colonies showed a moderate correspondence between them (table 1). However, no significant correlation was found between the measured environmental parameters (temperature and humidity) and any of the four colonies' foraging rhythms, suggesting that temperature and humidity are not the most important factors determining the foraging schedule in *E. opaciventre*.

The diet of *E. opaciventre* included both dead and live animal protein (table 2). Prey mean dry weight was 0.29 g (SD = 0.150, $n = 67$ items), which is approximately 17% of the dry weight of a worker. Termite workers were the most frequently collected item (figure 1), accounting for 50.7% of the records, which corresponds to 42.7% of the total biomass collected by the ants. The second most important item was leaf-cutting ants, which comprised 19.4% of the records and 17.6% of the total
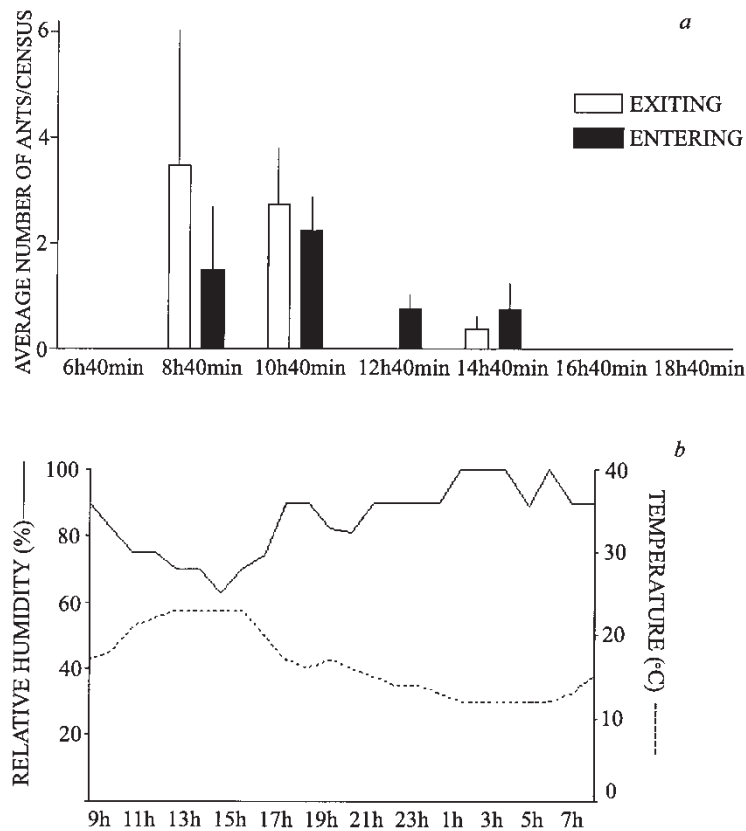

Fig. 3. Daily activity pattern of *Ectatomma opaciventre* in the cerrado of Itirapina, southeast Brazil, July 1998. Data result from 24 h of observations in four colonies: (a) number of ants in each period (mean + SE); (b) climate data.

Table 1. Spearman's correlation coefficients (*r*) between the daily foraging rhythms of four *E. opaciventre* colonies with each other, and with environmental parameters, and associated probabilities (*p*).

		Colony 2	Colony 3	Colony 4	Temperature	Humidity
Colony 1	*r*	0.3430	0.8531	0.6800	0.5681	0.4660
	p	0.2751	0.0004[†]	0.0150[†]	0.0540	0.1268
Colony 2	*r*		0.3316	0.6862	0.5243	0.3348
	p		0.2923	0.0137[†]	0.0802	0.2875
Colony 3	*r*			0.4931	0.4633	0.4171
	p			0.1034	0.1293	0.1773
Colony 4	*r*				0.4470	0.3422
	p				0.1452	0.2762
Temperature	*r*					0.9393
	p					0.0000

[†]Means at the 0.05 level. See details in text.

Table 2. Categories and abundance of food items collected by workers of *Ectatomma opaciventre* during the dry season, during 19 h and 30 min of observations, in the cerrado of Itirapina, south-east Brazil.

Item	Relative abundance	Mean dry weight (g)	Total biomass[†]	Pitfall traps
Termite worker	34 (50.7%)	0.25	42.71	9 (22.0%)
Atta sp.	13 (19.4%)	0.27	17.64	13 (31.7%)
Termite soldier	6 (9.0%)	0.38	14.17	0 (0%)
Coleoptera	6 (9.0%)	0.22	11.46	17 (41.5%)
Insect parts	3 (4.5%)	0.94	6.63	0 (0%)
Other ants	2 (3.0%)	0.33	3.32	2 (4.9%)
Cydnid hemipteran	1 (1.5%)	0.41	2.06	0 (0%)
Plant matter	1 (1.5%)	0.37	1.86	0 (0%)
Araneae	1 (1.5%)	0.03	0.15	0 (0%)
Total	67			41

Values are absolute records; relative frequencies are given between parentheses.
[†]Abundance × weight.

biomass. We observed the cleaning activity of a nest, during which the workers brought out several insect carcasses. These carcasses were brought to the laboratory and observed under a dissecting microscope. In addition to the items in table 2 we could add two additional coleopteran species and one ant species (*Camponotus rufipes*).

Data from pitfall traps suggest *E. opaciventre* foragers did not collect the food items according to their availability in the environment. One beetle species, which comprised only 8.9% of the food items collected by the foragers, accounted for 41.4% of the items collected by the pitfall traps. This may result from the high escape capacity of these beetles, since on several occasions we were able to observe unsuccessful predation attempts by *E. opaciventre*. On the other hand, the low frequency of termites could be due to an artefact of the pitfall trap sampling technique, since these insects have a very restricted spatial distribution and low epigaeic activity. In fact, most of the termites collected were close to the opening of their colonies.

When encountering a potential food item, *E. opaciventre* behaved according to the nature of the item. When detecting a food item, usually at a distance of 1–2 cm, the forager would stay motionless for a few seconds. After this short period, the ant began to inspect the prey with the antennae. Harmless prey, such as termite workers and dead insects, were simply seized with the mandibles and brought directly to the nest. On the other hand, when dealing with dangerous prey, such as *Atta* workers and termite soldiers, *E. opaciventre* foragers were more cautious, taking longer to attack and stinging the prey one to several times before bringing them to the nest.

If the prey moved away from the forager, or escaped after the first strike, the ant usually increased its searching behaviour, as well as the speed and sinuosity of the path ('reserve behaviour' *sensu* Dejean, 1988). This behaviour has been observed in other species, and its function has been associated with the possibility of collecting a wider variety of sizes and types of prey (Dejean, 1988; Dejean *et al.*, 1993). Reserve behaviour was particularly useful in collecting the fast and agile ground beetles.

We found no evidence of recruitment in the field. Foragers carry a single food item each time, the size of which is limited to what the ant is able to carry alone. On one occasion we observed a worker trying to carry a dead mantid back to the nest (about three times the size of the forager), but after nearly 40 min the ant gave up and returned to the nest.

The nests of *E. opaciventre* occur at a density of 0.015 nests per m^2 (figure 2). The nest dispersion pattern showed a significant tendency towards over-dispersion ($Z = 2.95$, $p = 0.0016$, $n = 14$ nests), with a mean nearest-neighbour distance of 5.85 m and an aggregation index of 1.482. The most complex microenvironments, such as the categories 'tall herbs' and 'bushes + palms', were preferred by *E. opaciventre* as nesting sites ($p < 0.0001$ and $p = 0.0015$, respectively; Z tests for proportions). Simpler microenvironments such as 'small grasses' were avoided ($p < 0.0001$; Z test for proportions), whereas 'bare sand' was neither rejected nor preferred ($p = 0.4286$; Z test for proportions).

The map of the foraging routes clearly shows that *E. opaciventre* has individual foraging area fidelity (figure 4). Each ant forager explores repeatedly a particular
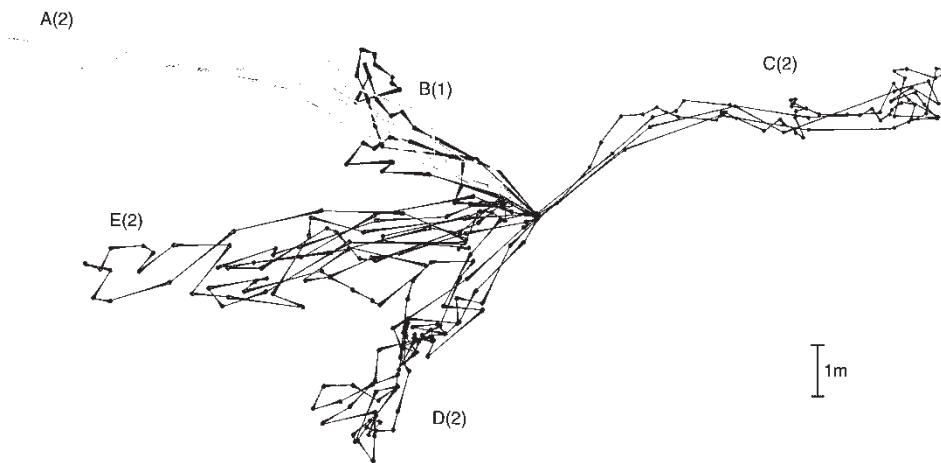

FIG. 4. Foraging routes of *Ectatomma opaciventre* foragers from one colony. Each letter represents one individual ant, and values indicate number of paths recorded for each forager. The routes from each forager are depicted in different shades of grey.

portion of the colony's foraging area, with little overlap with the routes of other workers. A successful forager's route is depicted in figure 5. The ant usually has a meandering path, which continues until she returns to the nest if no food item is found. On the other hand, if a food item is found and captured, the ant returns directly to the nest in a nearly straight path.

Discussion

A primarily diurnal foraging rhythm is common to many species closely related to *E. opaciventre*, such as *E. permagnum*, *E. ruidum* and *E. brunneum* (= *quadridens*) (Overal, 1986; Paiva and Brandão, 1989; Pratt, 1989; Passera *et al.*, 1994), although slight seasonal variations may occur (Lachaud, 1990). A decrease in the foraging activity at the hottest hours of the day, forming a characteristic bimodal foraging rhythm, is also observed in several ponerines (cf. Overal, 1986; Dejean and Lachaud, 1994; Duncan and Crewe, 1994; Passera *et al.*, 1994). A primarily nocturnal foraging pattern may also occur in *Ectatomma*, as reported for *E. tuberculatum* (Wheeler, 1986; Valenzuela-González *et al.*, 1995). Even though a primarily diurnal foraging activity is common to many ponerine species, in general some activity remains during the night (Breed and Bennet, 1985; Pratt, 1989), particularly if associated with honeydew-producing hemipterans, as observed in *E. ruidum* (Passera *et al.*, 1994)
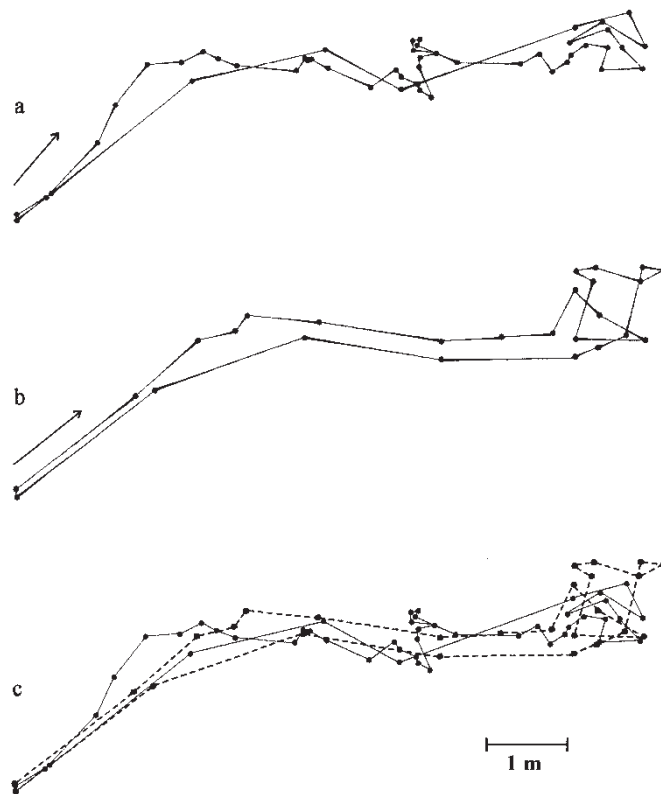

FIG. 5. Diagram showing the foraging paths of the same forager of *Ectatomma opaciventre* (worker C from figure 4) on two different days, indicating their overlap. Note that the outbound path has very little overlap with the inbound path. (a) First trip; (b) second trip; (c) combination of both trips. See text for details.

and *E. edentatum* (Del-Claro and Oliveira, 1999). In *E. opaciventre* foraging activity during the study period was restricted to only a few hours during the day, possibly due to the extremely reduced number of foragers in this species, an unique trait of *E. opaciventre*. The data shown in this study suggest that temperature and humidity may not be the main factors constraining this pattern, given the lack of correlation between these parameters and the foraging activity.

Most studies on ant diet are based on the food items brought to the nest by foragers (Fresneau, 1985; Paiva and Brandão, 1989; Valenzuela-González *et al*., 1995). Wheeler (1986) used this method to study *E. tuberculatum* and asserted that this species is able to subdue large and aggressive prey, although the author does not report having witnessed any predation event. This kind of assertion sustains the notion that ponerine ants are essentially predators (e.g. Carrol and Janzen, 1973; Fernández, 1991). Accordingly, the present study shows that *E. opaciventre* feeds opportunistically both as a predator or a scavenger, a common trait in the genus *Ectatomma* (Pratt, 1989; Lachaud, 1990; Valenzuela-González *et al*., 1995; Lachaud *et al*., 1996).

The diet found for *E. opaciventre* appears to be the least diverse ever recorded for an *Ectatomma*. Lachaud (1990), studying *E. ruidum*, registered 19 types of food items. Among these, 28.8% corresponded to carbohydrate-rich liquid foods, such as extrafloral nectar, hemipteran honeydew and fruit pulp (Lachaud, 1990). A similar situation was found in the diet of *E. tuberculatum*, in which liquid food (extrafloral nectar and honeydew) can account for 35.5% of the successful foraging trips (Valenzuela-González *et al*., 1995). The absence of extrafloral nectar in the diet of *E. opaciventre* is further confirmed by the absence of any record of this species feeding on extrafloral nectar, even though surveys of ant communities associated with extrafloral nectaries has been the topic of intensive research in areas where *E. opaciventre* is known to occur (e.g. Oliveira and Brandão, 1991; Del-Claro and Oliveira, 1999; personal observation).

It is noteworthy that, as in *E. opaciventre*, one of the most frequent food items of *E. ruidum* were also ants, which accounted for 18.8% of the food items in the dry season and 17.2% in the rainy season (Lachaud, 1990). This pattern also occurred in *E. permagnum*, whose diet is composed mostly of alates and workers of *Pheidole*, and of workers of *Camponotus* (Paiva and Brandão, 1989). Ants are also important food items in *E. tuberculatum* (Lachaud *et al*., 1996) and in the closely related genus *Gnamptogenys* (Pratt, 1994). Wheeler (1986) also observed the presence of ants (*Odontomachus*, *Pheidole*, *Azteca*, *Camponotus*) in the diet of *E. tuberculatum*. The low diversity of food items in the diet of *E. opaciventre*, however, was not caused by high selectivity by the ant, but rather by the low diversity of food items available in the environment. This was confirmed in the laboratory, where *E. opaciventre* workers accepted promptly other kinds of items, such as *Tenebrio molitor* larvae and pieces of *Nauphoeta cinerea* (Pie, 2002).

According to the classification of Beckers *et al.* (1989), *E. opaciventre* has a foraging strategy called individual or diffuse foraging, where there is no systematic co-operation or communication in the search, retrieval or transport of food items. This strategy is particularly suitable for *E. opaciventre*, since the food items in its diet were distributed in the environment in a unpredictable way, both in time and space (Carrol and Janzen, 1973; Duncan and Crewe, 1994). This strategy is common in other species in this genus, such as *E. ruidum* and *E. bruneum* (Overal, 1986; Lachaud, 1990; Passera *et al*., 1994). Nevertheless, these *Ectatomma* species are able

to recruit nestmates (Overal, 1986; Pratt, 1989; Breed *et al.*, 1990; Schatz *et al.*, 1997), a behaviour absent in *E. opaciventre*. In *E. ruidum* there is graded recruitment to rich or difficult food sources (Schatz *et al.*, 1997). One possible explanation for the absence of recruitment in *E. opaciventre* is that it is not necessary, since all the food items present in the study site could be carried by a single worker. Our field observations indicate that a foraging ant does not recruit, even if the prey is too big to be carried individually. Indeed, laboratory experiments in which colonies of *E. opaciventre* were starved for several days and then provided a variety of food sources (honey; artificial diet; cockroach—in three treatments: live but immobilized, dead and in pieces) failed to demonstrate recruitment behaviour (M. R. Pie, unpublished). Nevertheless, some social facilitation may occur (Wilson, 1971; Lachaud, 1985; Peeters and Crewe, 1987), i.e. the return of individual foragers may increase activity inside the nest. This may cause other workers to exit the nest to search for food themselves, even though neither trail laying nor any directional information conveyance were present, as observed in other ponerine species (e.g. *Pachycondyla goeldii*, Orivel *et al.*, 2000; *E. ruidum*, Lachaud, 1985).

Foragers of *E. opaciventre* specialize in particular foraging zones, thus enabling the simultaneous exploration of a wider foraging area for the colony. This kind of spatial fidelity is called *path fidelity*, and has already been previously observed in other ponerines (Uezu, 1977; Lachaud *et al.*, 1984; Fresneau, 1985; Dejean *et al.*, 1993; Schatz *et al.*, 1995; Fourcassié *et al.*, 1999). The term path fidelity was first proposed by Rosengren (1971), meaning the tendency of individual foragers to prefer one determined foraging route amongst a number of alternatives (Rosengren and Fortelius, 1986). In this strategy the foragers specialize in exploring individual 'sub-territories', to which they come recurrently. This enables them to orient quickly to food resources, and also to return to the nest quickly (Traniello, 1989; Beugnon and Fourcassié, 1988; Beugnon and Dejean, 1992). This strategy also reduces the time effort in the search for food, as well as external constraints to foraging, such as disorientation or attacks by competitors or predators (Wehner *et al.*, 1983). Indeed, it is noteworthy that, when disturbed, foragers of *E. opaciventre* run to their respective foraging area, which suggests that familiarity with foraging grounds is important against predators. Fresneau (1985) proposed a simple mechanism to explain path fidelity in individual foragers: during the first excursions, new foragers select a preliminary foraging path. The path can be confirmed when the forager captures the first prey, and by a simple learning process by reinforcement the path is maintained in future journeys. Even though this is a good explanation for the maintenance of stable foraging routes, this hypothesis does not explain how the foraging areas of individual foragers are kept discrete. Some observations on *E. opaciventre* may clarify this aspect. Whenever workers from the same colony met in the foraging area, both ants performed mutual antennal drumming on each other's head before spreading apart to different routes. This simple mechanism could induce a forager to diminish the search for food in areas that are also being used by other foragers, and therefore increases the efficiency of the foraging at the colony level. However, additional field observations on this and other species are necessary to confirm this hypothesis.

The local density of nests in the genus *Ectatomma* can vary widely. There are records of nest densities in *E. ruidum* from 0.14 nests per m^2 (Breed *et al.*, 1990) to 1.06 nests per m^2 (Pratt, 1989). Paiva and Brandão (1989) found a density of 0.148 nests per m^2 in *E. permagnum*, almost 10 times higher than the one found here for

E. opaciventre (0.015 nests per m²). Wheeler (1986), studying *E. tuberculatum* in Panama, found a density of 0.06 colonies per m². Despite these differences in the local densities, ant nests are usually found to be overdispersed (Levings and Franks, 1982; Wheeler, 1986). An overdispersed nest spacing pattern has been suggested in several studies as an indication of intraspecific competition (Ryti and Case, 1986). In *E. opaciventre* the number of active foragers was extremely reduced to the extent that encounters between workers from different colonies was indeed rare. Therefore direct interactions between foragers from different colonies is unlikely to cause the colonies' over-dispersed pattern. Our results lend support to microhabitat choice as a candidate mechanism to explain this pattern, since most nests were preferably located in more complex microhabitats. However, alternative mechanisms such as predation on founding queens (Ryti and Case, 1986) could also play a role, since the strategy of partially claustral nest founding is typical in the genus *Ectatomma* (Dejean and Lachaud, 1992).

Acknowledgements

References

Antonialli-Junior, W. F. and Giannotti, E., 1997, Nest architecture and population dynamics of the Ponerinae ant, *Ectatomma opaciventre* Roger (Hymenoptera, Formicidae), *Journal of Advanced Zoology*, **18**, 64–71.
Baroni Urbani, C., Bolton, B. and Ward, P. S., 1992, The internal phylogeny of ants (Hymenoptera: Formicidae), *Systematic Entomology*, **17**, 301–329.
Beckers, R., Goss, S., Deneubourg, J. L. and Pasteels, J. M., 1989, Colony size, communication and ant foraging strategy, *Psyche*, **96**, 239–256.
Beugnon, G. and Dejean, A., 1992, Adaptive properties of the chemical trail system of the African weaver ant *Oecophylla longinoda* Latreille (Hymenoptera, Formicinae), *Insectes Sociaux*, **39**, 341–346.
Beugnon, G. and Fourcassié, V., 1988, How do red wood ants orient during diurnal and nocturnal foraging in a three dimensional system? II. Field experiments, *Insectes Sociaux*, **35**, 106–124.
Bolton, B., 1995, *A New General Catalogue of the Ants of the World* (Cambridge, MA: Harvard University Press), 504 pp.
Breed, M. D. and Bennet, B., 1985, Mass recruitment to nectar sources in *Paraponera clavata*, a field study, *Insectes Sociaux*, **32**, 198–208.
Breed, M. D., Abel, P., Bleuze, T. J. and Denton, S. E., 1990, Thievery, home ranges and nestmate recognition in *Ectatomma ruidum*, *Oecologia*, **84**, 117–121.
Brown, W. L., Jr., 1958, Contributions toward a reclassification of the Formicidae. II Tribe Ectatomminae (Hymenoptera), *Bulletin of the Museum of Comparative Zoology at Harvard*, **118**, 175–362.
Carrol, C. R. and Janzen, D., 1973, Ecology of foraging by ants, *Annual Review of Ecology and Systematics*, **4**, 231–257.
Clark, P. J. and Evans, F. C., 1954, Distance to the nearest neighbor as a measure of spatial relationships in populations, *Ecology*, **35**, 281–290.
Dejean, A., 1988, Failure as an effective stimulus of a 'reserve behavior' which allows the capture of alternative prey by *Serrastruma serrula* workers (Formicidae, Ponerinae), *Sociobiology*, **4**, 325–339.
Dejean, A. and Lachaud, J.-P., 1992, Growth-related changes in predation behavior in

incipient colonies of the ponerine ant *Ectatomma tuberculatum* (Olivier), *Insectes Sociaux*, **39**, 129–143.

DEJEAN, A. and LACHAUD, J.-P., 1994, Ecology and behavior of the seed-eating ponerine ant *Brachyponera senaarensis* (Mayr), *Insectes Sociaux*, **41**, 191–210.

DEJEAN, A., BEUGNON, G. and LACHAUD, J.-P., 1993, Spatial components of foraging behavior in an african ponerine ant, *Paltothyreus tarsatus*, *Journal of Insect Behavior*, **6**, 271–285.

DEL-CLARO, K. and OLIVEIRA, P. S., 1999, Ant–Homoptera interactions in a neotropical savanna: the honeydew-producing treehopper *Guayaquila xiphias* (Membracidae) and its associated ant fauna on *Didymopanax vinosum* (Araliaceae), *Biotropica*, **31**, 135–144.

DUNCAN, F. D. and CREWE, R. M., 1994, Field study on the foraging characteristics of a ponerine ant, *Hagensia havilandi* Forel, *Insectes Sociaux*, **41**, 85–98.

FERNÁNDEZ, F., 1991, Las hormigas cazadoras de genero *Ectatomma* (Hymenoptera, Formicidae) en Colombia, *Caldasia*, **16**, 551–564.

FOURCASSIÉ, V., HENRIQUES, A. and FONTELLA, C., 1999, Route fidelity and spatial orientation in the ant *Dinoponera gigantea* (Hymenoptera, Formicidae) in a primary forest, a preliminary study, *Sociobiology*, **34**, 505–524.

FRESNEAU, D., 1985, Individual foraging and path fidelity in a ponerine ant, *Insectes Sociaux*, **32**, 109–116.

FRESNEAU, D., GARCIA-PÉREZ, J. and JAISSON, P., 1982, Evolution of polyethism in ants: observational results and theories, in P. Jaisson (ed.) *Social Insects in the Tropics* (Paris: Presses de l'Université Paris-Nord), Vol. 1, pp. 129–155.

GIANNOTTI, E., 1988, Composição florística e estrutura fitossociológica da vegetação de cerrado e de transição entre cerrado e mata ciliar da Estação Experimental de Itirapina (SP). Master's thesis, Universidade Estadual de Campinas, Campinas, SP, Brazil.

GOODLAND, R., 1971, A physiognomic analysis of the cerrado vegetation of central Brazil, *Journal of Ecology*, **59**, 411–419.

HÖLLDOBLER, B. and WILSON, E. O., 1990, *The Ants* (Cambridge, MA: Belknap Press of Harvard University Press), 732 pp.

HOUSTON, A., SCHMID-HEMPEL, P. and KACELNIK, A., 1988, Foraging strategy, worker mortality, and the growth of the colony in social insects, *The American Naturalist*, **131**, 107–114.

KEMPF, W. W., 1972, Catálogo abreviado das formigas da região neotropical (Hymenoptera, Formicidae), *Studia Entomologica*, **15**, 3–344.

KREBS, C. J., 1989, *Ecological Methodology* (New York: Harper and Row Publishers), 654 pp.

KUGLER, C. and BROWN, W. L., JR., 1982, Revisionary and other studies on the ant genus *Ectatomma*, including the descriptions of two new species, *Search*, **24**, 1–7.

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., 1990, Foraging activity and diet in some Neotropical ponerine ants. I. *Ectatomma ruidum* Roger (Hymenoptera, Formicidae), *Folia Entomológica Mexicana*, **78**, 241–256.

LACHAUD, J.-P., FRESNEAU, D. and GARCÍA-PÉREZ, J., 1984, Etude des stratégies d'approvisionnement chez trois espèces de fourmis Ponérines (Hymenoptera, Formicidae), *Folia Entomológica Mexicana*, **61**, 159–177.

LACHAUD, J.-P., LÓPEZ-MÉNDEZ, J. A., SCHATZ, B., DE CARLI, P. and BEUGNON, G., 1996, Comparaison de l'impact de prédation de deux ponérines du genre *Ectatomma* dans un agroécosystème néotropical, *Actes des Colloques Insectes Sociaux*, **10**, 67–74.

LEVINGS, S. and FRANKS, N. R., 1982, Patterns of nest dispersion in a tropical ground ant community, *Ecology*, **63**, 338–344.

OLIVEIRA, P. S. and BRANDÃO, C. R. F., 1991, The ant community associated with extrafloral nectaries in Brazilian cerrados, in D. F. Cutler and C. R. Huxley (eds) *Ant–Plant Interactions* (Oxford: Oxford University Press), pp. 198–212.

ORIVEL, J., SOUCHAL, A. CERDAN, P. and DEJEAN, A., 2000, Prey capture behavior of the arboreal ponerine ant *Pachycondyla goeldii* (Hymenoptera: Formicidae), *Sociobiology*, **35**, 131–140.

OVERAL, W. L., 1986, Recrutamento e divisão de trabalho em colônias naturais da formiga *Ectatomma quadridens* (Fabr.) (Hymenoptera, Formicidae, Ponerinae), *Boletin do Museu Paraense Emílio Goeldi*, **2**, 113–135.

PAIVA, R. V. S. and BRANDÃO, C. R. F., 1989, Estudos sobre a organização social de *Ectatomma permagnum* Forel, 1908 (Hymenoptera, Formicidae), *Revista Brasileira de Biologia*, **49**, 783–792.

PASSERA, L., LACHAUD, J.-P. and GOMEL, L., 1994, Individual food source fidelity in the neotropical ponerine ant *Ectatomma ruidum* Roger (Hymenoptera, Formicidae), *Ethology, Ecology and Evolution*, **6**, 13–21.

PEETERS, C. and CREWE, R. M., 1987, Foraging and recruitment in ponerine ants, solitary hunting in the queenless *Ophthalmopone berthoudi* (Hymenoptera, Formicidae), *Psyche*, **94**, 201–214.

PERFECTO, I. and VANDERMEER, J. H., 1993, Cleptobiosis in the ant *Ectatomma ruidum* in Nicaragua, *Insectes Sociaux*, **40**, 295–299.

PIE, M. R., 2002, Behavioral repertoire, age polyethism and adult transport in *Ectatomma opaciventre* (Formicidae: Ponerinae), *Journal of Insect Behavior*, **15**, 25–35.

PRATT, S. C., 1989, Recruitment and other communication behavior in the ponerine ant *Ectatomma ruidum*, *Ethology*, **81**, 313–331.

PRATT, S. C., 1994, Ecology and behavior of *Gnamptogenys horni* (Formicidae, Ponerinae), *Insectes Sociaux*, **41**, 255–262.

ROSENGREN, R., 1971, Route fidelity, visual memory and recruitment behaviour in foraging wood ants of the genus *Formica* (Hymenoptera, Formicidae), *Acta Zoologica Fennica*, **133**, 1–106.

ROSENGREN, R. and FORTELIUS, W., 1986, Ortstreue in foraging ants of the *Formica rufa* group—hierarchy of orienting cues and long-term memory, *Insectes Sociaux*, **33**, 306–337.

ROSENGREN, R. and SUNDSTRÖM, L., 1987, The foraging system of a red wood ant colony (*Formica* s. str.)—collecting and defending food through an extended phenotype, *Experientia Supplement*, **54**, 117–137.

RYTI, R. T. and CASE, T. J., 1986, Overdispersion of ant colonies, a test of hypothesis, *Oecologia*, **69**, 446–453.

SCHATZ, B., and WCISLO, W. T., 1999, Ambush predation by the ponerine ant *Ectatomma ruidum* Roger (Formicidae) on a sweat bee *Lasioglossum umbripenne* (Halictidae), in Panama, *Journal of Insect Behavior*, **12**, 641–663.

SCHATZ, B., LACHAUD, J.-P. and BEUGNON, G., 1995, Spatial fidelity and individual foraging specializations in the Neotropical ant *Ectatomma ruidum* Roger (Hymenoptera, Formicidae), *Sociobiology*, **26**, 269–282.

SCHATZ, B., LACHAUD, J.-P. and BEUGNON, G., 1997, Graded recruitment and hunting strategies linked to prey weight and size in the ponerine ant *Ectatomma ruidum*, *Behavioural Ecology and Sociobiology*, **40**, 337–349.

TRANIELLO, J. F. A., 1989, Foraging strategies of ants, *Annual Review of Entomology*, **34**, 191–210.

TSCHINKEL, W. R., 1991, Insect sociometry, a field in search of data, *Insectes Sociaux*, **38**, 77–82.

UEZU, K., 1977, On the foraging activity of *Diacamma rugosus* (Le Guillon), *Biological Magazine Okinawa*, **15**, 5–17.

VALENZUELA-GONZÁLEZ, J., LÓPEZ-MÉNDEZ, A. and LACHAUD, J.-P., 1995, Activity patterns and foraging activity in nests of *Ectatomma tuberculatum* (Hymenoptera, Formicidae) in cacao plantations, *Southwestern Entomologist*, **20**, 507–515.

WEHNER, R., HARKNESS, R. D. and SCHMID-HEMPEL, P., 1983, *Foraging Strategies in Individually Searching Ants, Cataglyphis bicolor (Hymenoptera, Formicidae)* (Stuttgart: G. Fisher Verlag), 79 pp.

WHEELER, D. E., 1986, *Ectatomma tuberculatum*, foraging biology and association with *Crematogaster* (Hymenoptera, Formicidae), *Annals of the Entomological Society America*, **79**, 300–303.

WHEELER, W. M., 1910, *Ants, Their Structure, Development and Behavior* (New York: Columbia University Press), 663 pp.

WILSON, E. O., 1971, *The Insect Societies* (Cambridge, MA: Harvard University Press), 548 pp.