

Foraging ecology of the giant Amazonian ant *Dinoponera gigantea* (Hymenoptera, Formicidae, Ponerinae): activity schedule, diet and spatial foraging patterns

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This study provides a detailed account of the natural history and foraging biology of the ponerine ant *Dinoponera gigantea* in a rainforest in north Brazil. The species nests on the ground and the colonies contain 70–96 workers. Ant activity is negatively correlated with temperature, and is more intense at dawn and dusk. Foragers leave the nest independently and search for food individually on the leaf litter, within *ca* 10 m around the nest. Workers are opportunistic feeders that collect seeds and fruits, and hunt for live prey as well as scavenge for dead animal matter. The dry weight of food items ranges from <10 mg (spiders, insect parts) to >400 mg (seeds, fruits). There is no nestmate recruitment during the search for or retrieval of food, irrespective of food type and size. Foragers have a high directional fidelity, and ants from neighbouring colonies may engage in ritualized territorial contests at the border of their foraging areas. The foraging ecology of *D. gigantea* is compared with other ponerine species living in tropical forests, as well as with other ant groups showing similar behavioural patterns.

KEYWORDS: Activity rhythms, ants, *Dinoponera*, Formicidae, Ponerinae, spatial foraging patterns, territorial contests.

Introduction

Ants outnumber all other terrestrial organisms and occur in virtually all types of habitats (Wheeler, 1910). The dominance of ants is particularly conspicuous in the tropical region, especially in rainforests, where they account, together with termites, for nearly one-third of the entire animal biomass (Fittkau and Klinge, 1973). Foraging ants may search for solid or liquid food on the ground and/or on foliage, and the dietary requirements across different species within the family

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Formicidae is extremely diverse (Carroll and Janzen, 1973; Hölldobler and Wilson, 1990). Ants may also vary widely in the strategies they use to gather food, and foraging modes may range from solitary hunting in which there is no co-operation during search and food retrieval, to varying levels of co-operative foraging mediated by different degrees of recruitment communication between nestmates (Hölldobler and Wilson, 1990). Because the foragers usually depart from a fixed nest location, ants are regarded as useful organisms to test a number of hypotheses about foraging strategies. According to Traniello (1989), a full understanding of an ant colony's foraging system requires the determination of both the individual and social components of the foraging behaviour, as well as of the ecological setting in which the colony occurs (i.e. its resource and competitive environment). Therefore more natural history information and quantitative data are needed about the foraging characteristics of different species before we can properly assess the selective pressures underlying observed ant foraging systems.

A variety of foraging strategies occurs across different ant species in the primitive subfamily Ponerinae (Peeters and Crewe, 1987). Foraging modes range from solitary to group hunters, and from specialist to generalist predators (e.g. Hölldobler, 1982; Fresneau, 1985; Maschwitz *et al.*, 1989; Lachaud, 1990; Duncan and Crewe, 1994; Leal and Oliveira, 1995). Although generally regarded as predatory ants, ponerine species may also feed on extrafloral nectar, homopteran honeydew, secretions from lepidopteran larvae, as well as lipid-rich seeds (e.g. Horvitz, 1981; Hölldobler, 1985; DeVries, 1991; Oliveira and Brandão, 1991; Pizo and Oliveira, 1998; Del-Claro and Oliveira, 1999).

Species in the Neotropical ponerine genus *Dinoponera* are among the largest known ants. Workers attain a size of 3–4 cm in length (Kempf, 1971; Paiva and Brandão, 1995). They nest on the ground and are distributed throughout South America in several habitat types, ranging from arid savannas to rainforests (Kempf, 1971). *Dinoponera* species are queenless and reproduction is performed by mated workers (Dantas de Araujo *et al.*, 1990). Colony foundation may occur by fission (Overall, 1980). Despite their impressive size and local abundance, little is known about the foraging ecology of *Dinoponera* ants. Although the few available reports indicate that the ants are generalist predators on litter arthropods and snails (Fowler, 1985; Paiva and Brandão, 1995), to date there is no quantitative account on the diet or foraging behaviour of *Dinoponera*.

This paper presents a detailed field account on the foraging ecology of the Amazonian ant *Dinoponera gigantea*. Previous observations on this species indicate that workers forage individually and show some fidelity to a foraging area (Fourcassié *et al.*, 1999). We here provide further qualitative and quantitative data on the natural history and foraging biology of *D. gigantea*, with emphasis on colony demography, activity rhythms, dietary requirements and spatial foraging patterns.

Materials and methods

Field work was carried out during December 1999 (end of the dry season) in a secondary rainforest site located at the Fazenda Vitória, near Paragominas (2°59'S, 47°31'W), State of Pará, north Brazil. The physiognomy of the vegetation consisted of trees and palms (up to 30 m tall) and scattered understory shrubs (\approx 1–2 m tall) growing over a thick layer of leaf litter. Seventeen nests of *D. gigantea* were marked in the study area, and their main external characteristics were recorded (i.e. location, number and diameter of nest entrances). At the end of the behavioural observations

four nests were excavated to determine their depths and the demography of the colonies. Ant voucher specimens are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP).

Activity schedule

For three colonies (Nos 9, 10, 12) all individuals seen outside the nests during the course of the study were individually marked on the thorax and/or gaster with a distinct colour code, using dots of enamel paint (Testors Co., Rockford, USA). The nests of these colonies were 30–44 m apart from each other. Foraging rhythms at colonies Nos 9 and 10 were monitored continuously from dawn (6.00 a.m.) to dusk (6.00 p.m.). During the observation period all workers (marked and unmarked) exiting or entering each nest were recorded, and air temperature was monitored at 1-h intervals. The duration of foraging trips by marked workers was calculated based on their departure and arrival times. Short trips by workers engaged in maintenance activities were also recorded (i.e. removal of nest refuse, removal of sticks and leaves from nest entrance). Although returning workers transporting food items were not disturbed to avoid altering their foraging activity (see Stadling, 1978), some of the retrieved items were large enough to be identified on sight.

Survey of food items

The food items retrieved by *D. gigantea* were surveyed by removing them from the mandibles of returning foragers from any of the 17 marked nests, but mainly from nests Nos 9, 10 and 12. This procedure allowed the collection of a large number of food items. In cases where the removal of the item was avoided (see above), the identification of the food was included in the survey. Food items were preserved in 70% alcohol and brought to the laboratory for more detailed identification. The items were then kept in the oven at 60°C for 24 h, and their dry weights were measured with a Mettler H51Ar analytical balance.

Spatial foraging patterns

In order to assess the extent of the foraging range of the colonies and to investigate the spatial pattern of individual foragers, marked ants were followed as soon as they exited a nest by placing consecutively numbered flags along their paths at 1-min intervals (Turchin *et al.*, 1991). The position of the flags was then mapped by measuring their distances relative to two reference points, and by using triangulation formulae. Ants were followed for up to 15 min. Preliminary observations have shown that the maximum distance from the nest was generally reached within this period. We measured the spatial specialization of individual foragers by computing the mean vector of the distribution of the azimuth relative to the nest of all the fixes composing their paths (Batschelet, 1981). The statistical significance of the mean vector was assessed by using the Rayleigh test. A significant vector indicates that the fixes are not randomly distributed around the nest, but are instead concentrated in a narrow angular sector.

Results

Natural history and demography

Except for one isolated nest, all other nests of *D. gigantea* were located at the base of trees ($N=12$), palms ($N=2$) or thick lianas ($N=2$). The nests' external

appearance was conspicuous on the forest floor because their immediate vicinity was usually surrounded by yellowish soil particles due to excavation by the ants, which however, did not form a mound. Each nest had one to eight entrances (mean \pm SD = 3.9 ± 2.3 ; $N = 17$) of 3–8 cm in diameter, which were 3–250 cm apart from each other. The four excavated nests were shallow (≈ 40 cm deep), with chambers *ca* 3-cm high and 20-cm wide. When in close proximity to each other (< 10 cm apart), the entrances normally merged into a single gallery *ca* 15 cm below the soil surface, which led to the nest chambers. On the other hand, nest entrances which were 40–250 cm apart had no connection underground, indicating that *D. gigantea* has also polydomous nesting habits (i.e. colony occupies more than one nest; see Hölldobler and Wilson, 1990). The demographic data of the colonies from the excavated nests are shown in table 1. The colonies were reproductively active, and contained a significant amount of brood during the study period. The marking procedure revealed that 27–40% of the workers were engaged in activities outside the nest (i.e. maintenance, or foraging).

Activity rhythms and diet

The activity rhythms of monitored colonies was negatively correlated with temperature (colony No. 9: $r_s = -0.83$, $P < 0.01$; colony No. 10: $r_s = -0.78$, $P < 0.01$). Ant activity presented a bimodal distribution and was more intense at dawn and dusk, just before and after the period of maximum temperature for the day (figure 1). However, since ants were also seen returning to the nest at sunrise, and leaving at sunset, some activity presumably also occurred during the night period. Foraging activity during the 12-h sampling was performed by 23–24% of the workers in each colony, as revealed by the records of individual marked ants in proportion to the total number of ants per colony (determined after nest excavations). Ants typically leave the nest independently and search for food individually within a radius of *ca* 10 m around the nest (see below). Qualitative observations, however, suggest that the ants' foraging range may occasionally surpass this limit, since ants were attracted to sardine baits placed *ca* 20 m from their nests. Foragers usually walk towards one direction for 15–20 min, after which they begin to search around for food within a limited area. Such foraging trips could last up to 3 h, but ants usually found prey items within 30–60 min (figure 2). In both colonies only 10% of the foraging trips were successful during the 12-h sampling. Brief trips (≤ 5 min) around the immediate vicinity of the nest were very frequent and consisted mostly of maintenance activities

Table 1. Composition of four *Dinoponera gigantea* colonies, determined by excavation at the end of the behavioural observations carried out in secondary Amazonian rainforest, north Brazil, in December 1999.

Colony code	No. of workers	No. of pupae	No. of larvae	No. of eggs	No. of males	No. of workers marked (%)
9	70	15	18	0	1	25 (35.7)
10	95	38	5	0	8	38 (40.0)
11	75	27	19	6	2	–
12	96	5	7	11	0	26 (27.1)

Colonies contained 84.0 ± 13.4 workers (mean \pm SD). Except for colony No. 11, where no workers were marked, all workers engaged in activities outside the nest (i.e. maintenance, or foraging) were marked.

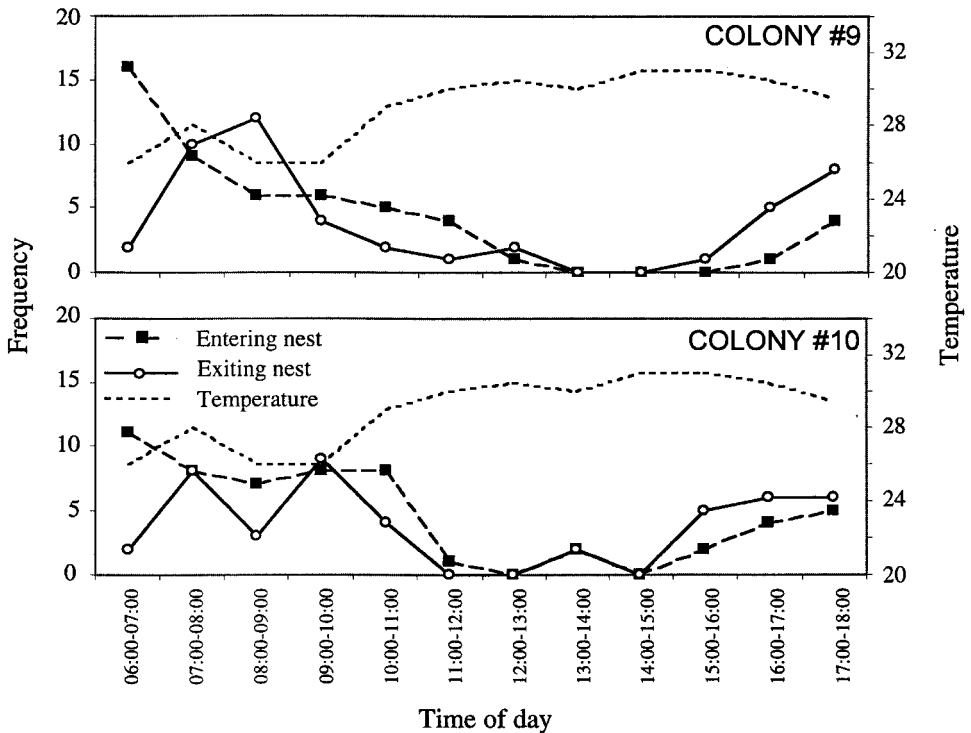


FIG. 1. Activity rhythm of two *Dinoponera gigantea* colonies in a secondary rainforest in north Brazil. Ant activity is more intense at dawn and dusk hours, before and after maximum temperature for the day.

such as the removal of nest refuse, or of sticks and leaves from nest entrances (figure 2).

Dinoponera gigantea forages exclusively on the ground, never searching on plants. There was no evidence of recruitment communication between nestmates in the search for or during retrieval of food, irrespective of the type of prey. Foraging workers are opportunistic feeders that collect plant resources, and both hunt for live prey as well as scavenge for dead animal matter (table 2). The ants included a wide array of food types in their diet, from seeds and fruits (22% of all retrieved items) to a taxonomically diverse assemblage of litter-dwelling organisms (table 2). The size spectrum of prey items was also extremely wide (figure 3), and their dry weights ranged from < 10 mg (e.g. ants, spiders, insect parts) to > 100 mg (e.g. fruits, crickets, snails). *Vismia* fruits (Clusiaceae) and *Inga* seeds (Leguminosae) were the heaviest food items retrieved by the ants (> 400 mg). Individual foragers were able to carry aloft small- to medium-sized food items, and drag large ones through the leaf litter.

Spatial foraging patterns

A total of 67 tracks from 36 individual ants were recorded (colony No. 9: 21 tracks of 13 ants; colony No. 10: 24 tracks of 13 ants; colony No. 12: 22 tracks of 10 ants). Figure 4 shows the foraging range of each colony based on all tracks recorded. Except for colony No. 9, there was no directional bias in the foraging

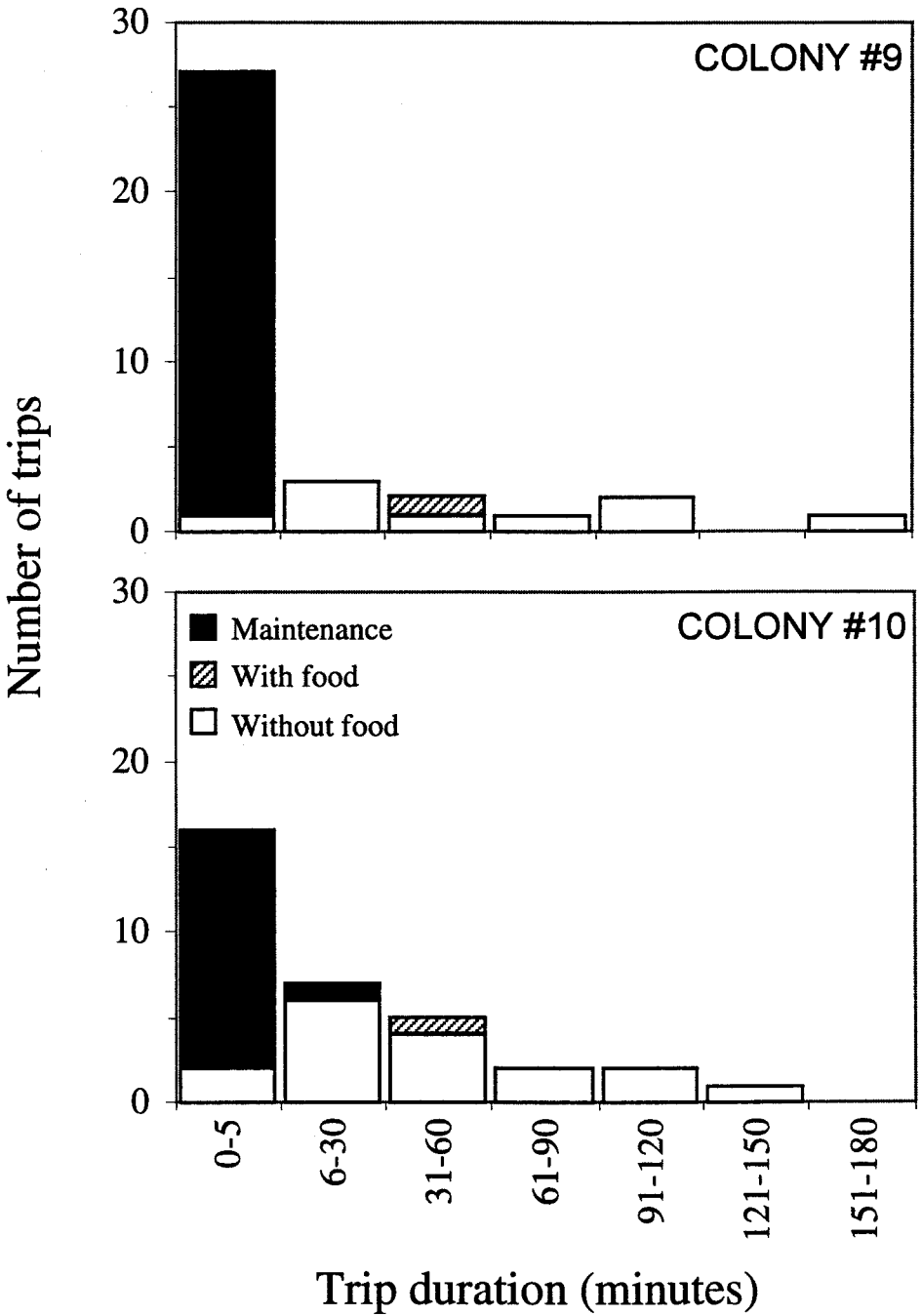


FIG. 2. Frequency distribution of trip duration relative to different activities performed by workers of *Dinoponera gigantea* in a Brazilian rainforest site. Although foraging ants may be away from the nest for up to 3 h, successful foragers usually return after 30–60 min of searching. Data are based on continuous 12-h observations at colony Nos 9 and 10, from 6.00 a.m. to 6.00 p.m. Two successful foragers from each colony are not included in the graphs because the duration of their foraging trips could not be recorded.

Table 2. List of food items collected by workers of *Dinoponera gigantea* in Amazonian rainforest in north Brazil, in December 1999.

Taxonomic identity of food item	No. of records (%), <i>n</i> =73 items	No. of live animal prey
Fungi		
Basidiomycetes (part of mushroom)	1 (1.4)	
Angiospermae		
Seed or fruit	16 (21.9)	
Insecta		
Orthoptera	8 (10.9)	7
Hymenoptera		
Vespidae	1 (1.4)	1
Formicidae	3 (4.1)	3
Isoptera	1 (1.4)	1
Coleoptera		
Adult	2 (2.7)	2
Larvae	2 (2.7)	2
Odonata	1 (1.4)	1
Blattodea	4 (5.5)	4
Homoptera		
Cicadellidae	1 (1.4)	
Cicadidae	1 (1.4)	1
Hemiptera		
Pentatomidae	1 (1.4)	1
Lepidoptera		
Adult	1 (1.4)	
Pupae	2 (2.7)	2
Larvae	2 (2.7)	2
Arachnida		
Araneae	2 (2.7)	2
Opiliones	2 (2.7)	
Chilopoda		
Scolopendromorpha (part of body)	1 (1.4)	
Diplopoda		
Polydesmida	1 (1.4)	
Turbellaria (part of body)	1 (1.4)	
Gastropoda		
Pulmonata	3 (4.1)	
Parts of arthropods	13 (17.8)	
Unidentified	3 (4.1)	

Food items were identified by removing them from returning foragers of several colonies, but mostly from colony Nos 9, 10 and 12. Collections were not made during systematic surveys of ant activity, so as not to alter the ants' foraging rhythm.

effort of the colonies. Within the 15-min observation period ants travelled *ca* 6 m (5.8 ± 3.0 ; $N=67$), at a maximum distance of 12.3 m from their nests (figure 4). The paths of individual ants that were followed at least twice during the study period are represented in figure 5 by distinct line patterns. The average period of time elapsed between two recorded tracks of the same ant was 3.5 days (range: 30 min to 9 days). Ants repeatedly visited the same zone and showed a high sectorial fidelity. This tendency is seen in the high significance of the mean vectors of the azimuths of the fixes of their paths (figure 5).

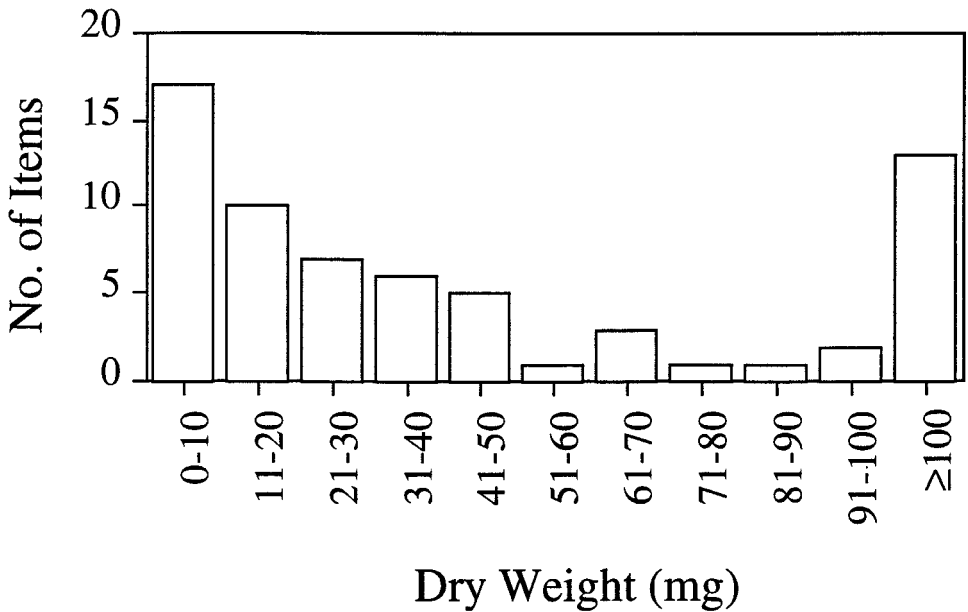


FIG. 3. Frequency distribution of the dry weights of food items ($N=66$) retrieved by *Dinoponera gigantea* foragers in a secondary rainforest, north Brazil.

Territorial behaviour

When two ants from different colonies met at the border of their foraging areas they engaged in a ritualized territorial contest that could last nearly 30 min. During such agonistic encounters the ants usually faced each other frontally and locked their mandibles together (figure 6A). While locked to one another the ants elevate the anterior part of their bodies, vigorously antennate each other's head, and constantly kick one another with the forelegs. Eventually one of the ants became dominant and stood over its opponent, which was dragged away. As the contest escalated the dominant ant was observed to bite her subordinate on the head, and direct the tip of the gaster against the opponent's body (figure 6B). The ants may then have fought briefly, with the subordinate ant walking away after breaking free. No injury to either ant was detectable after such contests.

Discussion

The period in which ants can be active is largely determined by the species' physiological properties, in particular by their tolerance limits with respect to temperature and humidity oscillations in the environment (Hölldobler and Wilson, 1990). The activity rhythm of *D. gigantea* was negatively associated with temperature and followed a bimodal pattern in which most activity is confined to early morning and late afternoon, with a marked decline around midday. Such an activity pattern is commonly seen in warm environments, and is also exhibited by other ponerine species living in tropical forests (Lévieux, 1977; Dejean and Lachaud, 1994; Duncan and Crewe, 1994; Passera *et al.*, 1994).

In general, the colonies of *D. gigantea* distributed their foraging effort fairly evenly around their nest. Some sectors, however, were visited less by the ants and this may be due to heterogeneities in the distribution of food resources (Levings,

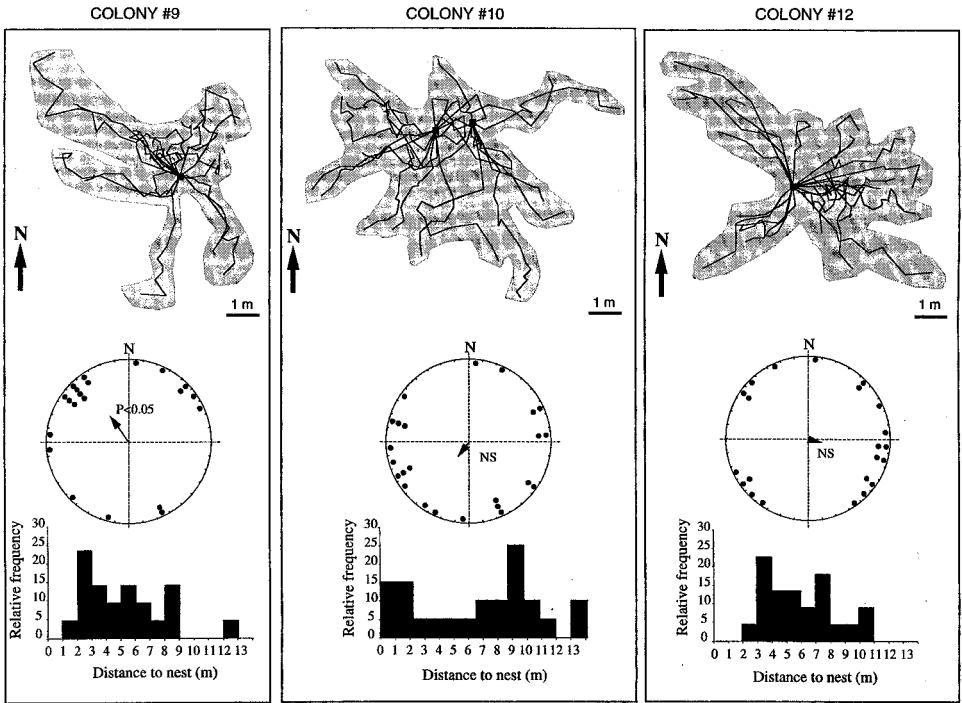


FIG. 4. Maps showing the spatial foraging patterns of the three colonies of *Dinoponera gigantea* studied in a Brazilian rainforest. The hatched area around all the recorded tracks represents the foraging range. The position of the nest entrances is indicated by a black square (note that colony No. 10 had two nest entrances). For each colony a circular graph shows the distribution of the direction of the last fix of the tracks. The radius of the circle corresponds to unity. The mean vector of the distribution is significant for colony No. 9 only (Rayleigh test). The frequency histograms at the bottom give the distance to the nest of the last fix of each of the tracks.

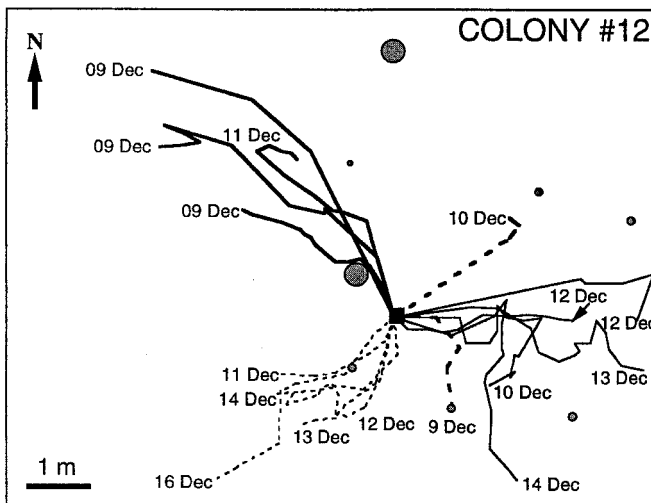
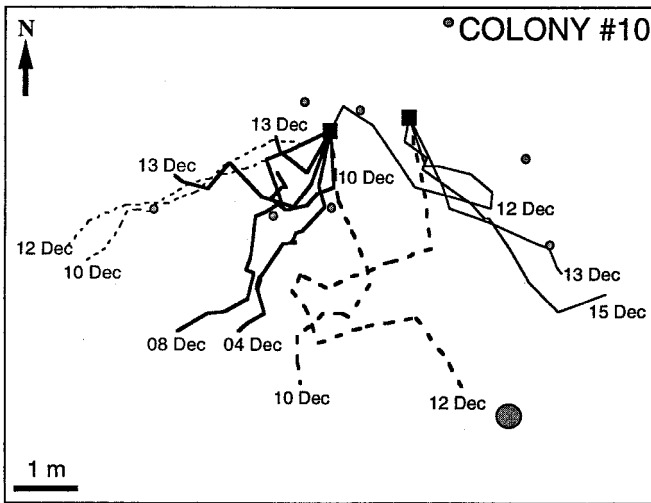
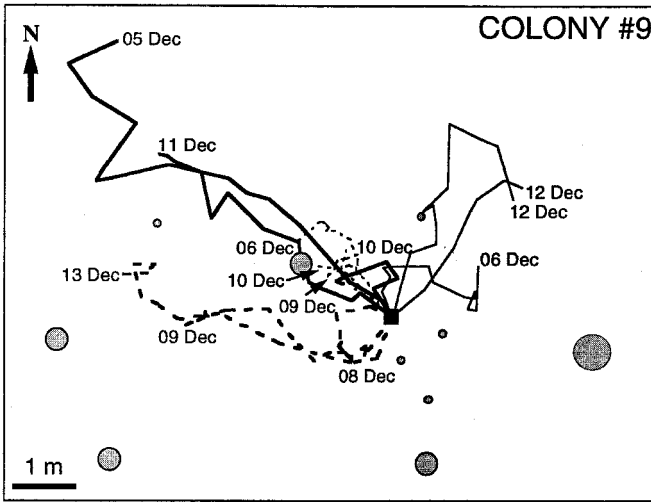
1983), or to competition effect due to neighbouring colonies (see below). *Dinoponera gigantea* typically exhibits an individual foraging strategy (Beckers *et al.*, 1989). Foragers independently hunt on live ground-dwelling organisms, and search for plant resources and dead animal matter within the leaf litter. This pattern has also been reported for several other ponerine species (Fresneau, 1985; Lachaud, 1990; Duncan and Crewe, 1994; Passera *et al.*, 1994; Ehmer and Hölldobler, 1995). However, as opposed to some solitary-hunting ponerines that may co-operate in prey retrieval (Hölldobler, 1984; Oliveira and Hölldobler, 1989; Pratt, 1989; Dejean *et al.*, 1993), no recruitment behaviour has ever been observed in *D. gigantea* while searching for or retrieving food. Foragers depart from their nest repeatedly in the same direction and prospect for food within a restricted sector around their nest. Some individuals persisted visiting the same limited area for periods of up to 9 days. This result complements that of Fourcassié *et al.* (1999) showing that homeward *D. gigantea* foragers use the same route through the vegetation over a 3-week period.

Occasional observations of foragers returning with food items show that they spend less time in the nest than unsuccessful foragers, and that they return directly to and search at the location of their last food find (see also Duncan and Crewe, 1994). Harkness and Maroudas (1985) and Deneubourg *et al.* (1987) have shown

with two different mathematical models that this simple spatial reinforcement process can lead at the individual level to a high spatial fidelity and at the colony level to a partitioning of the foraging ground among workers. Such a spatial foraging pattern has been described in several ant species searching solitarily for dispersed food items (*Pogonomyrmex maricopa*: Hölldobler, 1976; *Cataglyphis bicolor*: Wehner *et al.*, 1983; Schmid-Hempel, 1987; *Pachyconyla apicalis*: Fresneau, 1985; *Ocymyrmex velox*: Wehner, 1987; *Formica schaufussi*: Traniello, 1988; *Paltothyreus tarsatus*: Déjean *et al.*, 1993a; *Hagensia havilandi*: Duncan and Crewe, 1994; *Odontomachus bauri*: Ehmer and Hölldobler, 1995; *Messor arenarius*: Warburg, 1996). Solitarily searching ants can rely exclusively on path integration or on spatial memory to orient in their environment. In heterogeneous environments with a dense canopy cover such as tropical forests, navigation by path integration is likely to be difficult to implement since the celestial cues necessary to integrate the directional components of the paths are only visible intermittently. Therefore ants have to navigate by using their memory of the visual landmarks encountered along familiar routes (Baader, 1996; Fourcassié *et al.*, 1999). The directional fidelity observed in these ants may thus be constrained by the cost of being lost when they wander away from their familiar sector. According to Wehner (1987), a forager ant is the less likely to abandon the direction of a preceding unsuccessful trip the more successful foraging trips it has achieved in the same direction. Solitary searching ants would consequently develop directional fidelity only if they have a high rate of reinforcement (i.e. if their foraging efficiency is high). The low foraging efficiency observed in *D. gigantea* colonies suggests, however, that the cost of being lost may be strong enough a constraint to prevent the ants from visiting unfamiliar neighbouring sectors. Navigational constraints may thus be ultimately more important than ecological constraints in shaping the spatial foraging pattern of individual foragers (Fewell, 1990).

External activities related to nest maintenance and foraging involved 27–40% of the *D. gigantea* workers, whereas in the African ponerine *Hagensia havilandi* such tasks are performed by 60–77% of the worker force (Duncan and Crewe, 1994). The proportion of workers involved in foraging was also smaller in *D. gigantea* (23–24%) than in *H. havilandi* ($\approx 40\%$; Duncan and Crewe, 1994). Foraging efficiency, as expressed by the proportion of foraging trips resulting in food retrieval, was lower in *D. gigantea* (10%) than in *H. havilandi* in Africa (37%; Duncan and Crewe, 1994), *Ectatomma ruidum* in Mexico (12–19%; Lachaud, 1990) and *Odontomachus bauri* in Panama (28%; Ehmer and Hölldobler, 1995). Three factors, however, need to be taken into account in these comparisons. First, Lachaud (1990) has shown that foraging efficiency varies seasonally and that during the dry period *E. ruidum*'s average success rate decreases from 19 to 12%. Second, in the dry season *E. ruidum* collects liquid food on plants, and if only solid food is considered the species' foraging efficiency drops to 10% (Lachaud, 1990), as also reported here for

FIG. 5. Maps showing the tracks of *Dinoponera gigantea* foragers that were followed at least twice during the study period. Each line pattern corresponds to a different ant. The labels on the side of the lines indicate the date at which the tracks were recorded. The nests are represented by a black square. The main trees are symbolized by grey circles whose diameter is roughly proportional to that of the trees. The circles on the right show the mean vector of the azimuths of the fixes composing the paths of each ant. The radius of the circle corresponds to unity. All vectors are highly significant ($P < 0.01$, Rayleigh test).



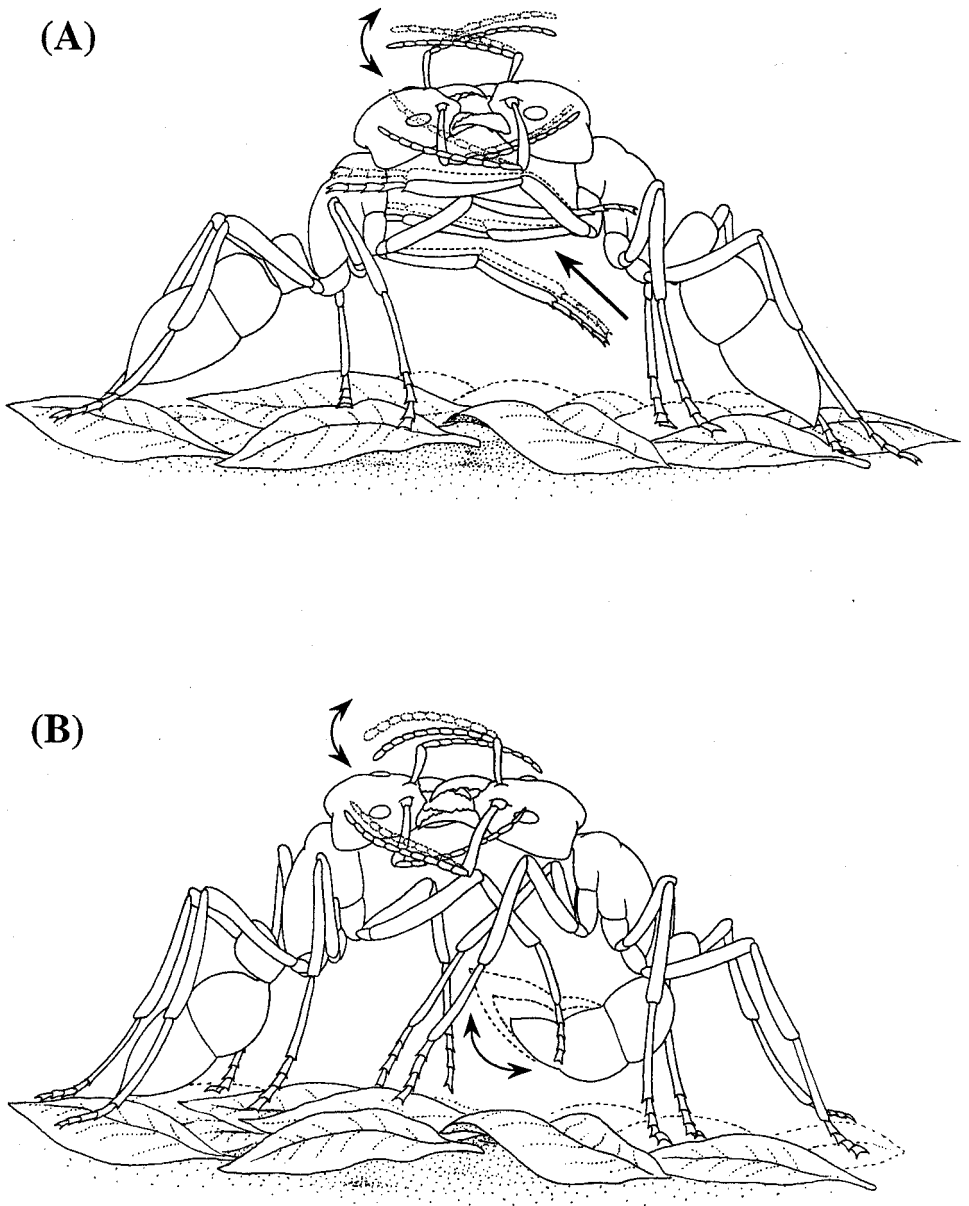


FIG. 6. Ritualized territorial contest between *Dinoponera gigantea* foragers from different colonies at the border of their foraging areas. (A) Ants lock their mandibles together, vigorously antennate each other's head, and constantly kick one another with the first pair of legs. (B) As the contest escalates the dominant ant (right) directs the tip of the gaster against the opponent's body. The subordinate ant eventually walks away as she breaks free.

D. gigantea in the dry period. Third, *D. gigantea* is a very large ant that is able to capture and transport very large food items. On the other hand, smaller ponerines such as *Hagensia*, *Ectatomma*, *Pachycondyla* and *Odontomachus* (1.0–1.5 cm in length), search for prey that correspond to their more limited load-carrying capacities

(Lachaud, 1990; Duncan and Crewe, 1994; Ehmer and Hölldobler, 1995; Medeiros, 1997; Pie, 1998). About 50% of the prey items retrieved by *D. gigantea* have dry weights > 30 mg, and the individual foragers were seen transporting food items twice their own weight (> 400 mg). Large prey items (i.e. cockroaches, cicadas) are much less abundant than small ones (i.e. ants, termites) on the floor of tropical forests (Levings and Windsor, 1984). Moreover, as opposed to small prey and persistent liquid food sources (i.e. nectar, honeydew), large prey items are usually more difficult to find, subdue and transport by an individual forager. Despite their huge size, *D. gigantea* ants may take up to 15 min to drag a large prey to the nest, and during retrieval the forager risks losing the food item to mass-recruiting myrmicine ants such as *Crematogaster* and *Pheidole*.

Dinoponera gigantea foragers collect a wide diversity of food items within a variable size range. The taxonomic diversity of the food in *D. gigantea*'s diet roughly corresponds to that recorded for other ponerine species living in tropical forests (Fresneau, 1985; Lachaud, 1990; Dejean *et al.*, 1993b; Duncan and Crewe, 1994; Pratt, 1989; Ehmer and Hölldobler, 1995). Although ponerines are generally regarded as carnivorous ants, seeds and fruits comprised an important part (22%) in *D. gigantea*'s diet. Other ponerine genera such as *Ectatomma*, *Brachyponera*, *Pachycondyla*, *Odontomachus* and *Rhytidoponera* may also depend largely on seeds and fruits to complement their diets, and this in turn may affect the dispersal ecology of the plants (Davidson and Morton, 1981; Horvitz, 1981; Lachaud, 1990; Dejean and Lachaud, 1994; Pizo and Oliveira, 1998, 2000).

The avoidance or defeat of enemies is regarded as an important component in the foraging ecology of ants (Hölldobler and Wilson, 1990). Although the ritualized territorial contests reported here for *D. gigantea* follow the same pattern described for species in the ant subfamilies Formicinae, Dolichoderinae and Myrmicinae (reviewed by Hölldobler and Wilson, 1990), to our knowledge this is the first study to document such behavioural interactions in a ponerine species. Interestingly, the paired territorial contests observed in *D. gigantea* resemble the intracolony agonistic interactions associated with dominance hierarchies already described for ponerines, including *Dinoponera* (Oliveira and Hölldobler, 1990; Medeiros *et al.*, 1992; Monnin and Dantas de Araujo, 1995). Since colony founding in *Dinoponera* may occur by fission (Overall, 1980), it is possible that aggression between colonies becomes progressively more intense as the distance between them increases (see also Fowler, 1985).

How important is body size in explaining the foraging ecology of *D. gigantea*? Larger ants have lower mass-specific energetic costs but higher absolute gross costs of transport and this may influence their foraging decisions (Lighton *et al.*, 1987). In regard to this question it is interesting to compare the foraging ecology of *D. gigantea* with that of the equally big Old World species *Camponotus gigas* (length \approx 3 cm, weight \approx 400 mg; Pfeiffer and Linsenmaier, 2000). This formicine is commonly found in the rainforest of South-East Asia, a biotope that closely resembles the native environment of *D. gigantea*. *Camponotus gigas* has monogynous colonies containing about 7000 workers with two distinct subcastes of major and minor workers, and a highly polydomous structure (Orr and Charles, 1994; Pfeiffer and Linsenmaier, 1998, 2000). One major difference between the two species is that the diet of *C. gigas* consists of 87% honeydew (Pfeiffer and Linsenmaier, 2000) whereas this type of food is completely absent in *D. gigantea*. In the latter species energy intake is only provided by arthropod prey, seeds and fruits. These items require

longer foraging distances and their search, retrieval and transport are generally much more time consuming than liquid food. Seeds and prey, however, have higher energetic content than nectar, and this results in a higher ratio of energetic benefit relative to cost (Fewell *et al.*, 1996). In *C. gigas* the polydomous structure of the colonies allows curtailment of the high energetic costs of liquid food collection by reducing the homeward travel time of loaded workers: food is first carried by the foragers to the peripheral nests of the colony and from there subsequently transported to the central nest of the queen by a caste of specialist transport workers (Pfeiffer and Linsenmaier, 1998). Although *D. gigantea* colonies appear to be weakly polydomous, a higher degree of polydomy may be prevented in this species by the absence of a queen, and the necessity to maintain a reproductive hierarchy within mated workers (see Monnin and Dantas de Araujo, 1995).

According to Fewell (1988), ants that are characterized by a high ratio of energetic benefit relative to cost (such as *D. gigantea*) should choose foraging strategies that maximize net foraging gains per unit time, independently of absolute differences in foraging costs. This prediction seems to be supported by at least two components of the foraging strategy of *D. gigantea*. First, the partitioning of foraging ground among foragers of a colony reduce search time by preventing excessive overlap in the area scanned by individual workers. Second, foragers tend to select larger food items even if their transport incurs a larger cost.

In conclusion, our results on the foraging ecology of *D. gigantea* are in accordance with the prediction of Goss *et al.* (1989) that large solitary-foraging ants should perform better than small ones if they can memorize the location of the last food source, and if the prey items they collect are large relative to their size. The current study illustrates the importance of collecting basic quantitative data on the natural history, behaviour and ecology of an animal species of particular interest in order to test predictions generated by foraging models.

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