ECOLOGY, BEHAVIOR AND BIONOMICS

Foraging Behavior of the Queenless Ant *Dinoponera quadriceps* Santschi (Hymenoptera: Formicidae)

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Comportamento de Forrageio da Formiga sem Rainha *Dinoponera quadriceps* Santschi (Hymenoptera: Formicidae)

RESUMO - A procura e ingestão de alimentos são essenciais para qualquer animal, que gasta a maior parte de sua vida procurando os recursos alimentares, inclusive mais que outras atividades como acasalamento, disputas intra-específicas ou fuga de predadores. O presente estudo tem como objetivo descrever e quantificar diversos aspectos do forrageamento, dieta e transporte de alimentos em *Dinoponera quadriceps* Santschi em mata atlântica secundária do Nordeste do Brasil. Foram observadas três colônias escolhidas ao acaso distantes pelo menos 50 m uma das outras. Ao sair da colônia, as operárias eram seguidas até o seu retorno à mesma, sem nenhum provisionamento alimentar, nem interferência sobre suas atividades. As atividades utilizando técnica de *focal time sampling* com registro instantâneo a cada minuto, durante 10 minutos consecutivos. Cada colônia era observada 1 dia/semana, com pelo menos 6 h/dia resultando em 53,8h de observação direta das operárias. Foram registradas as atividades de forrageamento, o sucesso no transporte do alimento, tipo de alimento, limpeza e as interações entre operárias. O forrageio foi sempre individual não ocorrendo recrutamento em nenhuma ocasião. A dieta foi composta principalmente de artrópodes, sendo na maioria insetos. Em pequena proporção, ocorreu coleta de pequenos frutos de *Eugenia* sp. O tempo de forrageio foi maior quando as operárias transportavam alimentos até a colônia, sendo o período de retorno inferior ao de forrageio, sugerindo a utilização de pistas químicas e visuais na orientação, durante suas atividades de forrageio e coleta de alimentos.

PALAVRAS-CHAVE: Forrageamento, dieta, orientação

ABSTRACT - The search for and ingestion of food are essential to all animals, which spend most of their lives looking for nutritional sources, more than other activities such as mating, intra-specific disputes or escaping from predators. The present study aims to describe and quantify several aspects of foraging behavior, diet and food transport in the queenless ant *Dinoponera quadriceps* Santschi in a secondary Atlantic forest, Northeastern Brazil. Three colonies were randomly selected at a distance of at least 50 m from one another. On leaving the colony, worker ants were followed until their return, with no nutritional provision or interference with their activities. Activities were recorded using focal time sampling with instantaneous recording every minute for 10 consecutive minutes. Each colony was observed 1 day/week, for at least 6 h/day resulting in 53.8h of direct observation of the workers. Foraging activities, success in transporting food, type of food, cleaning and interaction among the workers were recorded. Foraging was always individual, with no occurrence of recruitment. Diet was composed mainly of arthropods, mostly insects. The collection of small fruits (*Eugenia* sp.) was also observed. Foraging time was greater when workers transported food to the colony, the return time being shorter than the foraging period, suggesting the use of chemical and visual cues for orientation during their foraging and food-collecting activities.

KEY WORDS: Foraging pattern, diet, orientation

The ecological success of a species depends on its ability to adjust the foraging strategies to maximize food intake with the least amount of energy possible (Stephens & Krebs 1971). Daily foraging adjustments are influenced mainly by limitations such as availability and space-time distribution of the food resource, as well as nutritional needs (Manly *et*

al. 1993, Giraldeau & Caraco 2000).

The investment in foraging of each ant colony depends on the ability and efficiency of each worker, on environmental changes, and on factors such as distance to the food source and demographic density (Gordon 1999, Silva & Noda 2000). Therefore, a difference in the investment and efficiency of each colony is expected. For the social insects, efficient foraging depends on own actions as well as on those of other individuals of the colony. The social foraging efficiency of social insects such as ants is not easy to measure because of the difficulty in identifying the efficiency of each individual (Giraldeau & Caraco 2000).

Different foraging strategies are used by ants based on environmental changes and food density (Fowler 1985, Herbers & Choiniere 1996). Foraging varies widely in the Ponerinae species, from solitary foraging to social foraging and from generalist to specialist predators (Peeters & Crewe 1987, Hölldobler & Wilson 1990, Leal & Oliveira 1995, Fowler 1997).

Ants consume a very diversified diet, including items of animal and vegetal origin as well as substances produced by fungi. Most ants exhibit generalist habits, consuming various types of animal or vegetal matter, although several species present more specialised feeding habits (Beugnon *et al.* 2001, Schatz *et al.* 2001). Formicids exhibit different levels of specialization when searching for and consuming food. Ponerinae feed on animals in the soil, such as colembolans, centipedes, millipedes, spiders and other insects, ants and termites included (Hölldobler & Wilson 1990, Schatz *et al.* 2001).

Dinoponera is formed by species with body size varying from 3 cm to 4 cm (Kempf 1971, Paiva & Brandão 1995). *Dinoponera* ants are described as solitary foragers with predominantly carnivorous habits, ranging from humid forest soil to dry savannas (Kempf 1971, Fourcassié *et al.* 1999, Fourcassié & Oliveira 2002).

The purpose of the present study is to describe and quantify several aspects of foraging behavior, diet and food transport in queenless ants *Dinoponera quadriceps* Santschi in a secondary Atlantic forest, Northeastern Brazil.

Material and Methods

The study was performed in Nisia Floresta National Forest (FLONA) of the Brazilian Environment Institute (06º 05' S, 35º12'W), Rio Grande do Norte State, Brazil. FLONA is a 175-ha natural reserve with 80 ha occupied by secondary Atlantic forest. 50 ha consist of brushland and grassland; 40 ha are occupied by experimental *Swietenia* sp. and *Eucalyptus* sp. plantations and 5 ha by lodging and administration buildings and arboretums of native vegetal species (Santee & Arruda 1994).

Data were collected in the secondary Atlantic forest area, consisting of trees varying in height from 5 m to 14 m and with a large amount of lianas and bromeliads, besides underbrush vegetation. Substratum in the area was composed of leaves, branches and twigs.

Three *D. quadriceps* colonies were observed from May to October 2000. The colonies were randomly selected, at least 50 m from one another. Colonies had two or three entrances, with an approximate distance between them of 2 m; one of the entrances was selected as the initial fixed point for behavioral observation.

Upon leaving the colony, the worker was followed until its return, with neither food provisioning nor interference with its activities. Worker activities were registered using focal time sampling (Martin & Bateson 1994) with recordings at 1-min intervals for 10 min. Between two 10-min blocks, there was a 5-min interval. By the end of each hour away from the nest, four observation periods were achieved for each worker.

The workers had no individual markings to allow their identification. Therefore, it is possible that the same individual was examined more than once in a day. Each colony was observed once a week, for at least 6 h/day (range 6h to 10h) between 6:00 a.m. and 5:00 p.m. In the three colonies, 3,225 focal points were recorded, resulting in 53.8h of direct worker observation (colony A = 21.7h, B = 16.5h and C = 15.6h).

Foraging activities recorded were: success in food transport, cleaning and interactions among workers, in addition to types of food transported, and whenever possible, identification of animal or vegetal origin. As a way of estimating the investment of workers in foraging and food collecting activities, we analyzed the duration of food search and transport to the colony. Since no significant differences were found among colonies ($P > 0.05$), the data were grouped for statistical analysis and analyzed through non-parametric tests – Kolmogorov-Smirnov two-sample test (D), Wilcoxon matched pairs test (T) and Chi-square (χ^2). Significance level of $P \leq 0.05$ was adopted for all the tests.

Results

Workers spent most of their extranidal activity time foraging (92.5%), and the remainder in social interactions (1.5%) or cleaning their body (3.3%), mainly antennae and legs.

D. quadriceps workers exhibit slow locomotion, with antennae touching the substratum during foraging activity. When a worker detects a food item, it usually moves more quickly, with an intensification of antennal movements. On these occasions movements occur around a central point where the food was encountered. If the food was collected, which occurred in 76% of the cases, the worker moved back to the nest at a variable velocity, depending on the substratum and the food size. On several occasions workers were observed returning to the nest without transporting any food. On some of these occasions, following overnight rainfall, workers touched accumulations of water in fallen leaves with their mouthparts, seemingly to collect small amounts of liquid.

The workers collected various types of food, mainly items of animal origin (70.5%), of which 60.9% were insects (Table 1). The capture of live food items was observed only twice: an insect larva and an adult diptera. This item were not killed at the capture site, but rather transported to the nest struggling between the worker's mandibles. The estimated size of most food items was from 2 cm to 3 cm in length. Food of vegetal origin was composed of whole

Table 1. Food items collected by *D. quadriceps* workers in an Atlantic forest area in Northeastern Brazil.

Taxonomic identity of food item	No. of records (%)
Angiospermae	
Myrtaceae [*Eugenia* sp. (fruit)]	26 (24.76)
Seed unidentified	5 (4.76)
Insecta	
Coleoptera	2 (1.90)
Diptera	3 (2.86)
Hemiptera	3 (2.86)
Hymenoptera (Vespidae)	2 (1.90)
Lepidotera	1 (0.95)
Orthoptera (Tettigonidae)	2 (1.90)
Unidentified	
The animal as a whole	33 (31,43)
Larvae	6 (5.71)
Pupae	1 (0.95)
Parts of the animal	11 (10.48)
Arachnida (Araneae)	
The animal as a whole	2 (1.90)
Parts of the animal	3 (2.86)
Chilopoda	2 (1.90)
Diplopoda	1 (0.95)
Mollusca	1 (0.95)
Annelida (Oligochaeta)	1 (0.95)

Figure 1. Median duration of food search and return to the colony (min), with or without food in wild *D. quadriceps* workers.

Eugenia sp. fruit (approximately 1 cm in diameter) or its seeds, and small seeds from unidentified species (Table 1).

The duration of foraging was quite variable, ranging from 10 to 175 min. Foraging episodes which culminated in capture and transport of food lasted around 51.0 min (interquartil deviation- 25%: 18 min, 75%: 80 min), while foraging in which the worker returned to the nest without food lasted around 24 min (interquartil − 25%: 6 min, 75%: 70 min) (Fig. 1). The workers were successful in capturing and transporting food to the nest in 76% of foraging episodes recorded.

Duration of foraging was analyzed according to food type and these episodes were divided into two parts (search: nest-food, return: food-nest). The workers spent around 93% of foraging time searching for animal or vegetal food and only 7% on transporting it to the nest (T test, animal food < 0.05, vegetal food P < 0.03) (Fig. 2).

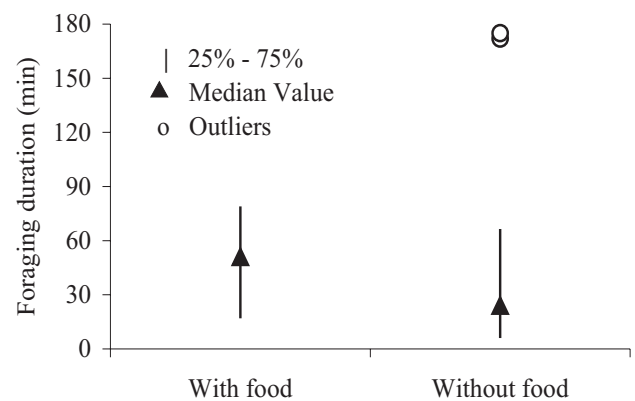**Discussion**

Behavioral strategies aimed at maximizing the amount of resources collected with the least amount of energy spent require adaptations in foraging behavior, mainly in social animals (Giraldeau & Caraco 2000). The results of this study indicate that queenless ant workers spend 95.2% of the time foraging. This finding was expected because search for food represents an important part of the workers' time budget and is essential to the survival of social insect colonies (Wilson 1971).

Corbara & Dejean (2000) indicate that *Pachycondyla analis* Latreille workers foraged in a solitary manner, but returned immediately to the nest to recruit dozens of new workers as soon as they found a group of termites. On this return trip to the nest the explorer leaves a chemical trail. After invading the termite nest, all the preys are transported to the ant nest. *Platythyrea modesta* Emery and *Polyrhachis laboriosa* Smith employ the same strategy as *P. analis*, differing only in the fact that these latter cut large preys into pieces before transporting them (Dejean *et al*. 1994, Djiéto-Lordon *et al*. 2001).

Cooperation among workers has never been observed in the capture or transport of food items. This absence of cooperation among workers during foraging is also pointed out in studies with *Dinoponera australis* Emery (Fowler 1985) and *Dinoponera gigantea* Perty (Fourcassié *et al*. 1999, Fourcassié & Oliveira 2002). Despite cooperation was not observed among the workers, several interactions were recorded among those from the same nest. In these interactions, two workers touched one another's antennae or head and then continued their foraging activity. In the cases, the workers likely belonged to the same nest. Fowler (1985) suggests that *D. australis* workers from nearby colonies are usually relatives, and for this reason they are more tolerant with workers from these colonies than they are with workers from distant ones.

D. quadriceps workers collected a wide variety of food, predominantly of animal origin (70%). Food items consisted of arthropods and on just a few occasions were these captured alive. At no time was animal food dismemberment prior to transport observed, but workers frequently carry body parts of dead arthropods. Of all arthropods captured, 61% were

Diptera or Orthoptera. The remainder consisted of Arachnida, Chilopoda, Diplopoda, Mollusca or Annelida. In this sense, the taxonomic diversity of *D. quadriceps* diet corresponds to other Ponerinae diets (Hölldobler & Wilson 1990). Comparing the data of this study with those presented by Fourcassié & Oliveira (2002), there is a strong coincidence (90%) in the presence of the same large groups of arthropods, which suggests a common diet pattern for genus *Dinoponera,* regardless of forest type.

Although Ponerinae are commonly presented as carnivores, in this study *D. quadriceps* workers transported small *Eugenia* sp. (Myrtaceae) fruit and small unidentified seeds. Similarly, Fourcassié *et al.* (1999) and Fourcassié & Oliveira (2002) indicate fruit and seed transport to the nest by *D. gigantea* workers. Some genera, such as *Ectatomma, Pachycondyla* and *Odontomachus* also include a considerable amount of fruit and seeds in their diets (Lachaud 1990, Pizo & Oliveira 2000).

The workers touch water accumulations with their mouthparts. If water collection did in fact occur, it was not possible to determine whether it was consumed or taken to the nest and regurgitated for the larvae and other workers. The transport of water to the colony during daily foraging is common in some wasps such as *Polybia occidentalis* Olivier (Hymenoptera: Vespidae) (Resende *et al.* 2001), and *Polistes ferreri* Saussure (Hymenoptera: Vespidae) (Silva & Noda 2000, Andrade & Prezoto 2001). The water collected is inserted into the cell walls to reduce temperature and can represent 36.5% of all material delivered to the colony on the hottest days (approximately 35º C) (Silva & Noda 2000, Andrade & Prezoto 2001).

The workers always left the colony at a relatively slow walking speed, initiating foraging a few centimeters from the entrance of the colony. However, workers that had found some type of food, returned quickly to the colony. Immediately after this first transport, the dynamics of the next trip underwent alterations, since they returned rapidly to the food site. When additional food was not encountered, they foraged for few minutes around this spot. If still nothing was found, the worker went foraging elsewhere. Lucas (unpublished data), in food provisioning experiments with queenless ant colonies in which workers were marked, reports that after transporting the first food item, the same worker rapidly returned to the food provisioning site on several successive occasions.

During foraging, workers performed this activity following meandering patterns until food items were found and captured. However, when transporting food back to the colony they followed an almost perfectly straight line, with small variations due to substratum characteristics. This return trip contrasted to the return to the nest without food, where the worker continued searching for food up to a distance of approximately 1 m from the colony. Nonetheless, we must point out that the capture of a food item was the indication to the observers of the end of the foraging episode, while returns to the nest without a food item did not have this indicator.

Food transport was reflected by different trip duration, characterized by longer trips when a food item was collected than when no food transport occurred. In principle, these results may be interpreted as resulting from food mass and transport difficulties encountered by the worker. However, trip duration when workers were transporting food was quite short when compared to total hunting time. The trip duration indirectly shows the level of investment of a worker in extranidal activities, especially in those related to the search and collection of food, since remaining up to 3h away from the nest implies considerable energetic expenditure and exposure to predation. Return trips to the nest with food further demonstrated the existence of an orientation system used by the workers, which allows them to optimize foraging time.

Fourcassié *et al.* (1999) indicate a return to the nest by *D. gigantea* workers during food transport in a manner
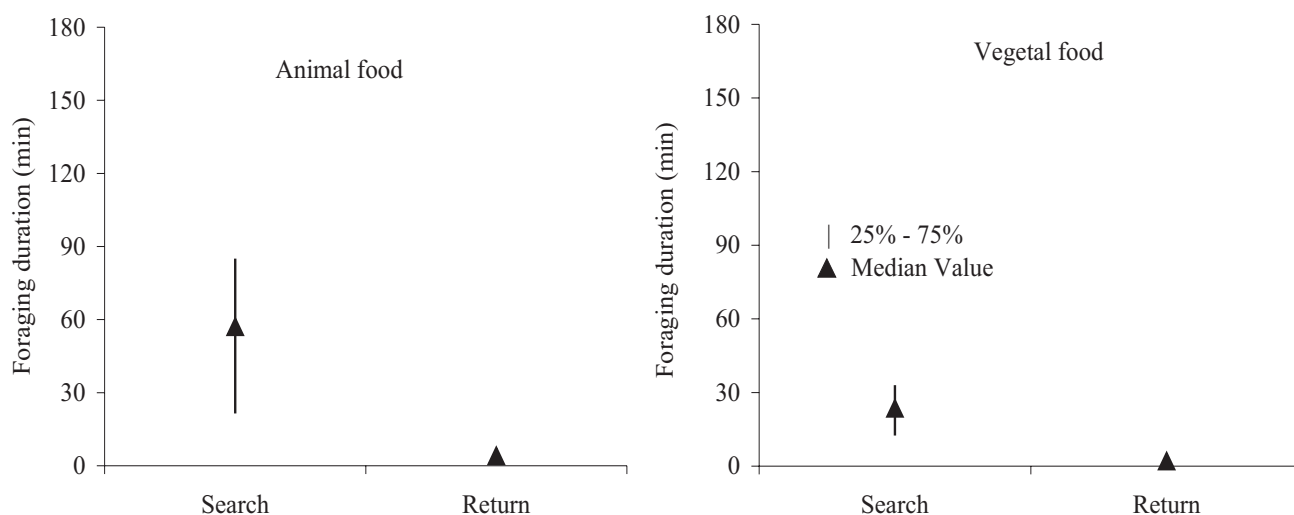

Figure 2. Median duration of foraging until prey capture (min) by wild *D. quadriceps* workers, according to food type.

similar to that reported above. These authors point out the possibility of the worker keeping visual markers such as trees, bushes, treetops, position of the sun and polarized light, in addition to chemical markers during extranidal activities. Despite changes in artificial markers and obstacles, *D. gigantea* workers corrected the route deviations toward the colony, demonstrating an integration of different sign perception systems. Wolf & Wehner (2000) describe an orientation system for *Cataglyphis fortis* Forel, which integrates olfactory, visual and anemotactic cues during extranidal activities.

Although no test was performed in relation to the orientation system, it is likely that *D. quadriceps* workers also use a system similar to that employed by *D. gigantea* and *C. fortis*, with the exception of anemotactic orientation. Several workers were observed rubbing the extreme lower portion of their abdomen on the substratum, supposedly during chemical marking. Although some workers performed this abdomen rubbing, marking regularly during foraging, the majority did not or did it at low frequency. If chemical material deposit by *D. quadriceps* workers in fact occurs in this study, the likely function is to establish individual trails, since no recruitment was observed.

The present study shows the existence of foraging and diet patterns in *D. quadriceps* similar to those observed in other species of the genus, based on solitary foraging with no recruitment or cooperation, and a diet based on the capture of animal food items. Despite *D. quadriceps* being considered a predatory species, our results demonstrated that the workers of this species preferentially forage dead organic material of animal origin.

Acknowledgments

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