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Foraging strategies of the ant *Ectatomma vizottoi* (Hymenoptera, Formicidae)

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ABSTRACT. Foraging strategies of the ant *Ectatomma vizottoi* (Hymenoptera, Formicidae). Foraging activity may be limited by temperature, humidity, radiation, wind, and other abiotic factors, all of which can affect energy costs during foraging. *Ectatomma vizottoi*'s biology has only recently been studied, and no detailed information is available on its foraging patterns or diet in the field. For this reason, and because foraging activity is an important part of the ecological success of social insects, the present study aimed to investigate *E. vizottoi*'s foraging strategies and dietary habits. First, we determined how abiotic factors constrained *E. vizottoi*'s foraging patterns in the field by monitoring the foraging activity of 16 colonies on eight different days across two seasons. Second, we characterized *E. vizottoi*'s diet by monitoring another set of 26 colonies during peak foraging activity. Our results show that *E. vizottoi* has foraging strategies that are similar to those of congeneric species. In spite of having a low efficiency index, colonies adopted strategies that allowed them to successfully obtain food resources while avoiding adverse conditions. These strategies included preying on other ant species, a foraging tactic that could arise if a wide variety of food items are not available in the environment or if *E. vizottoi* simply prefers, regardless of resource availability, to prey on other invertebrates and especially on other ant species.

KEYWORDS. Activity period; behavior; Ectatomminae; Insecta; nourishment.

Ants are poikilotherms, and their foraging activity is therefore limited by temperature, humidity, radiation, wind and other abiotic factors that might affect the time or energy costs of foraging (Traniello *et al*. 1984; Traniello 1989; Pol & Casenave 2004). Temperature is one of the primary factors affecting the foraging dynamics of many ant species. Higher temperatures increase ant metabolic rates, resulting in higher energy costs (Nielsen 1986). Traniello *et al.* (1984) observed that workers of *Formica schaufussi* Mayr, 1866 rejected smaller, less-profitable prey at low temperatures but accepted them at high temperatures. According to Heinrich (1993), humidity, the availability of food resources, and temperature, in particular, mediate the seasonal activity and daily movement of many insect groups.

Ants have very broad temperature ranges over which they are active (Heinrich 1993), though some species can forage more intensely at specific times of the day. McCluskey (1987) and Valenzuela-González *et al*. (1995) reported that the number of foragers of *Ectatomma tuberculatum* (Olivier, 1792) leaving the nest markedly increased at dusk. The number remained high during the first half of the night but dropped at dawn and remained low throughout the day. *Ectatomma ruidum* (Roger, 1860), on the other hand, showed the opposite pattern, with forager numbers high during the day and low at night (Lachaud *et al*. 1984; McCluskey 1987; Lachaud 1990).

Members of the genus *Ectatomma* Smith, 1858 are generalist predators that feed on a variety of small arthropods and annelids and may also collect extrafloral nectar and hemipteran honeydew (Fernández 1991; Oliveira & Brandão 1991; Del-Claro & Oliveira 1999; Pie 2004). In previous studies, it has been shown that *E. ruidum*, *E. tuberculatum*, *E. brunneum* Smith, 1858 and *E. opaciventre* (Roger, 1861) are generalists and can be dominant arboricolous or terricolous species in cocoa, coffee and maize plantations. They are both opportunistic predators and carrion-feeders, and most of the items they collect are arthropods (Pratt 1989; Lachaud 1990; Perfecto 1990; Giannotti & Machado 1992; Majer *et al.* 1994; Valenzuela-González *et al*. 1995; Lachaud *et al*. 1996; Ibarra-Núñez *et al*. 2001; Pie 2004; Tofolo *et al*. 2011).

The biology of *Ectatomma vizottoi* Almeida, 1987 has only recently been studied (Vieira *et al*. 2007, 2009, 2010, 2012), and a detailed investigation of the species' foraging patterns or diet in the field has yet to be conducted. For this reason, and because foraging activity is an important part of ecological success in social insects, the present study aimed to investigate the foraging strategies and dietary habits of *E. vizottoi.*

MATERIAL AND METHODS

The study was conducted from July 2009 to July 2010 in an area with 84 m² on the campus of the Mato Grosso do Sul State University (UEMS) in Dourados, Brazil (22°13'16''S; 54°48'20''W). At the site where the study took place, grass and shrub species are dominant. Mato Grosso do Sul has a humid, subtropical climate. The rainy season typically lasts from November through April, and the dry season lasts from May through October (Zavatini 1992).

In the first part of our study, we monitored the influence of three abiotic factors, temperature, humidity, and light intensity, on the fullest possible range of *E. vizzotoi*'s foraging activity throughout the year. Sixteen colonies were observed from 06:00 to 18:30 h on eight different days; observations were repeated four times during the dry season and four times during the rainy season. To avoid disturbing the colony foraging behavior during early nightfall, we used a lantern covered with red cellophane (Del-Claro 2004).

Two colonies were observed per day; each pair of colonies was located within a radius of two meters so that the observer could monitor one colony during the first 15 minutes of each hour and the second colony during the next 15 minutes. At every 15 minutes, the temperature (°C), relative humidity (%), and light intensity (Lux) were recorded during observations using a thermo-hygrometer and a photometer. During the observation period, the numbers of workers that left and entered the nest were recorded. Each of the 16 colonies was observed only once.

The forager efficiency index was calculated for the two seasons as follows: efficiency index = (number of incoming foragers carrying food x 100)/total number of incoming foragers (Giannotti & Machado 1992; Chagas & Vasconcelos 2002). To avoid influencing the intensity of colony foraging activity, we recorded the number of times foragers brought a given food item back to the nest, but we did not collect the food item.

The results were analyzed using Spearman's correlation analysis in the PAST program (Hammer *et al*. 2001). A regression tree was also used to determine which abiotic factors most influenced *E. vizzotoi*'s foraging activity; the number of ants foraging was the response variable and temperature, relative humidity, and light intensity were the explanatory variables. A regression tree was used to examine the influence of abiotic factors on harvesting success; the number of incoming foragers carrying food items was the response variable and temperature, relative humidity, and light intensity were the explanatory variables. The regression trees were generated using SYSTAT 10 software (Wilkinson 2000). They are constructed by repeatedly splitting the data according to a simple rule chosen based on a single explanatory variable. At each split, the data are partitioned into two mutually exclusive groups, each of which is as homogeneous as possible with respect to the response variable (De'ath & Fabricius 2000; Prasad *et al*. 2006). The output is a tree diagram with branches that are determined by the splitting rules and a series of terminal nodes that contain the mean response (Prasad *et al*. 2006).

In the second part of our study, we used the results obtained in the first part of the study to identify periods of peak foraging activity during the dry season and the rainy season. During these foraging peaks, we monitored a second group of 26 colonies for a total of 252 hours to characterize *E. vizottoi*'s diet; only one colony was monitored per day. During the first 15 minutes of each hour over a period of four hours, we collected the items that foragers brought to the nest. Prey items or other materials were removed from the mandibles of returning foragers with tweezers and preserved in 70% ethanol until further identification could take place.

RESULTS

The results of the Spearman's correlation analysis showed that temperature (P = 0.0029; R = -0.7527), relative humidity (P = 0.0092; R = 0.6888), and light intensity (P = 0.0305; R = -0.5989) were correlated with *E. vizottoi*'s foraging activity. However, the regression trees suggested that temperature was the most limiting factor (Fig. 1).

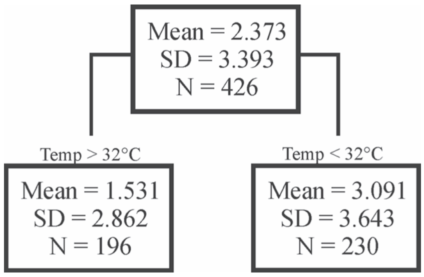

Fig. 1. Regression tree of the relationship between the number of foragers of *Ectatomma vizottoi* leaving the nest and temperature throughout the day.

When temperatures were below 32°C (Fig. 1), the number of workers involved in foraging activity was higher; however, no foraging activity was observed below 14°C. Furthermore, the mean number of incoming ants carrying food items was higher at temperatures below 32°C (Fig. 2).

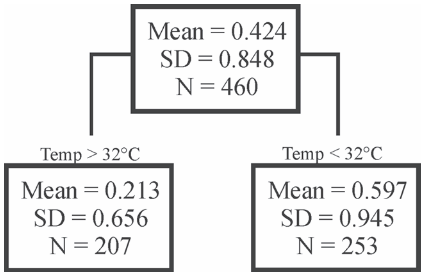

Fig. 2. Regression tree of the relationship between the number of incoming foragers of *Ectatomma vizottoi* carrying prey and temperature throughout the day.

Foraging activity peaked in the early morning from 07:00 to 09:30 h and in the late afternoon between 15:00 and 18:30 h and increased starting at nightfall, regardless of the season (Fig. 3). *Ecatomma vizottoi*'s efficiency index was 7.02% for the dry season and 11.36% for the rainy season.

Foragers collected mostly other species of ants, regardless of the season. Taken together, other species of ants composed 64.5% (n = 89) of the total sample (Tables I and II), which included species of *Camponotus* Mayr, 1861 (n = 63; 45.65% of the sample), *Pheidole* Westwood, 1839 (n = 17; 12.32% of the sample), *Azteca* Forel, 1878 (n = 4; 2.88%), *Brachymyrmex* Mayr, 1868 (n = 2; 1.44%), other species of *Ectatomma* (n = 2; 1.44%), and *Hypoponera* Santschi, 1938 (n = 1; 0.72%).

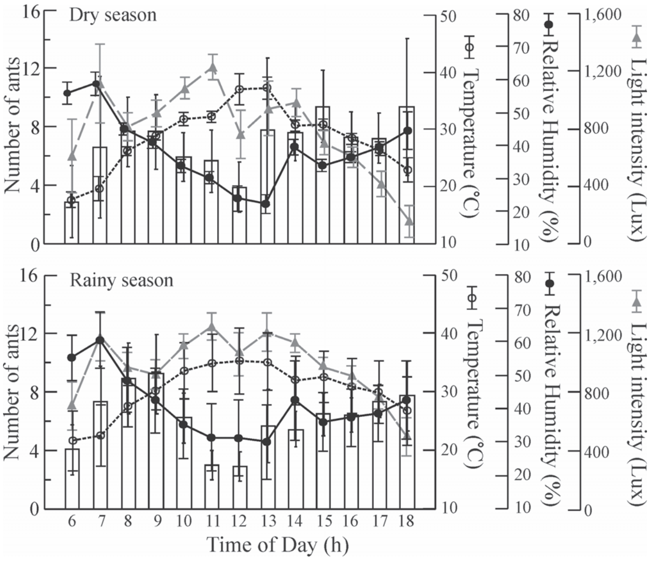

Fig. 3. Daily and seasonal variation in the foraging activity of 16 colonies of *Ectatomma vizottoi* in Dourados, Brazil. Colony activity was observed during the dry season (May-Oct) and the rainy season (Nov-Apr) from 06:00 to 18:30 h. Temperature (°C), relative humidity (%), and light intensity (Lux) were measured concurrently with foraging activity.

They also collected adults of other arthropod orders, including Isoptera, Arachnida, Diptera, Coleoptera, Orthoptera, Hemiptera, and other Hymenoptera as well as Lepidoptera larvae, and plant and animal material that could not be identified (Table I). Individual prey items were always intact, even when they were larger than the foragers. We always observed workers of *E. vizottoi* foraging alone, and we never observed any evidence of recruitment.

Table I. Food items collected by foragers of *Ectatomma vizottoi* in Dourados, Brazil in the dry season and rainy season in 2009 and 2010.

Food item	Dry season (May-Oct)	Rainy season (Nov-Apr)	Total
Arachnida	0	1	1
Coleoptera	1	3	4
Diptera	5	3	8
Hemiptera	1	7	8
Isoptera	4	3	7
Lepidoptera	4	3	7
Orthoptera	0	2	2
Other Formicidae	40	49	89
Other Hymenoptera	2	1	3
Unidentified items	1	8	9
Total	58	80	138

Table II. Ants collected by foragers of *E. vizottoi* in Dourados, Brazil during the dry season and rainy season in 2009 and 2010.

Ant species	Dry season (May-Oct)	Rainy season (Nov-Apr)	Total
Azteca sp.1	4	0	4
Brachymyrmex sp. 1	0	2	2
Camponotus sp. 1	8	7	15
Camponotus sp. 2	3	2	5
Camponotus sp. 3	3	1	4
Camponotus sp. 4	5	6	11
Camponotus sp. 5	1	1	2
Camponotus sp. 6	1	6	7
Camponotus sp. 7	1	0	1
Camponotus sp. 8	1	0	1
Camponotus sp. 9	2	0	2
Camponotus sp. 10	0	1	1
Camponotus sp. 11	0	2	2
Camponotus sp. 12	0	2	2
Camponotus sp. 13	1	4	5
Camponotus sp. 14	0	3	3
Camponotus sp. 15	2	0	2
Ectatomma sp. 1	0	1	1
Ectatomma sp. 2	0	1	1
Hypoponera sp. 1	1	0	1
Pheidole sp. 1	2	3	5
Pheidole sp. 2	4	3	7
Pheidole sp. 3	1	0	1
Pheidole sp. 4	0	4	4

DISCUSSION

The three abiotic factors we measured were correlated with foraging activity. However, since the regression trees suggested that foraging activity was primarily limited by temperature, relative humidity and light intensity likely indirectly influenced foraging activity because they covaried with temperature (Figs. 1, 2, and 3). Furthermore, abiotic factors such as temperature and humidity may interact with biotic factors such as resource availability and competition to generate different ant foraging activity patterns since both sets of factors may affect metabolic costs and therefore possibly influence prey selection (Traniello *et al*. 1984; Traniello 1989; Hahn & Wheeler 2002).

The Spearman's correlation analysis showed that foraging activity was negatively correlated with temperature and light intensity and positively correlated with relative humidity. The regression tree suggested that temperature had a crucial influence: *E. vizottoi* generally foraged at temperatures of 32°C or below. Once the temperature exceeded 32°C, foraging activity decreased (Fig. 1). However, there was also a minimal thermal limit since *E. vizottoi* did not forage at temperatures below 14°C. This result suggests that *E. vizottoi* foragers must avoid dehydration or other kinds of non-optimal conditions. However, it has been found that, even under laboratory conditions, *E. vizottoi*'s foraging activity peaks in the morning (Vieira *et al*. 2012). Therefore, it seems that this activity pattern is intrinsic in this species. It is also similar to activity patterns seen in congenerics, as Pie (2004) observed that *E. opaciventre* forages exclusively during the day and has two activity peaks: a larger peak in the morning and a smaller one in the afternoon. On the other hand, *E. tuberculatum* and *E. ruidum* forage at night even though they can also forage during the day (Lachaud *et al*. 1984; Wheeler 1986; McCluskey 1987; Pratt 1989; Lachaud 1990; Passera *et al*. 1994; Valenzuela-González *et al*. 1995).

Both dry season and rainy season efficiency indices for *E. vizottoi* were relatively similar to those found for *E. brunneum* (12.7%; Giannotti & Machado 1992) and *E.*

opaciventre (9.16%; Tofolo *et al*. 2011). In contrast, only the dry season indices of *E. vizottoi* resembled those found in *E. ruidum* and *E. tuberculatum*; in the rainy season, the efficiency indices of those two species were 20.3% and 19.4%, respectively (Lachaud *et al*. 1996). Although *E. vizottoi*'s efficiency index was similar across the two seasons, the greater availability of prey in the rainy season probably allowed ants to collect food items more easily (Lachaud *et al*. 1996). In fact, species-specific efficiency indices can vary due to many factors, such as environmental conditions, food resource availability, and variation in abiotic factors.

Our results show that most of the food items collected by *E. vizottoi* were other arthropods, especially ants (Tables I and II). Workers often used the strategy of foraging in vegetation near the nest to collect water that had accumulated on leaves and sugar-rich substances present in flowers and/or fruits. These substances also attract other insects upon which these ants often prey.

In previous studies of congenerics, most of the items collected were arthropods (Pratt 1989; Lachaud 1990; Giannotti & Machado 1992; Schatz & Wcislo 1999; Tofolo *et al*. 2011). Similarly, *E. tuberculatum* most frequently preyed upon other Formicidae and Hymenoptera (Valenzuela-González *et al*. 1995; Lachaud *et al*. 1996; Ibarra-Núñez *et al*. 2001). Although Pie (2004) found that *E. opaciventre* preyed exclusively or most frequently on termite workers, over 20% of the species' diet consisted of other ants, mainly *Atta* spp. Foragers belonging to the genera *Camponotus* and *Pheidole* are *E. vizottoi*'s most frequent prey (Table II). This observation can be explained by the abundance of these ants, which are among the most abundant genera worldwide and have varied foraging habits (Hölldobler & Wilson 1990) (Table I). In fact, *Ectatomma permagnum* Forel, 1908 was found to prey mostly upon *Pheidole* and *Camponotus* (Paiva & Brandão 1989).

Although more food items were collected in the rainy season (Table I), the variety of items collected during the two seasons was similar. These results contrast with those of Lachaud *et al*. (1996), who found that *E. ruidum*'s and *E. tuberculatum*'s diets were far more varied during the rainy season due to the large amount of prey available. Tofolo *et al*. (2011) hypothesized that *E. opaciventre* foragers brought back a low diversity of prey and other ants to the nest because prey variety and ant abundance was limited at the study site. The prey upon which this species primarily feeds may reflect its availability in the natural environment, and the relative amount of predation on a given prey species is generally proportional to that prey's relative abundance (Dejean 1991; Ibarra-Núñez *et al*. 2001).

According to Tofolo *et al*. (2011), *E. opaciventre* "prefers" other ants not because foragers are selective, but rather because food item diversity in the environment is low. This hypothesis has been supported by results from the laboratory: *E. opaciventre* workers readily accept other food items, such as mealworms, which are not found in their natural environment. However, *E. tuberculatum*'s "preference" for other ants does not reflect relative resource availability since sympatric *E. ruidum* has a very diverse diet; although both species have access to the same range of prey, they occupy different ecological strata (Lachaud *et al*. 1996).

Overall, foraging strategies seem to depend upon several ecological variables, such as the distribution of food resources in time and space, food size and quality, competition, and predation. A colony should therefore adopt a spatial foraging pattern that allows it to collect food effectively and minimize the chances of encountering competition, in order to minimize energy losses and maximize resource return per unit time (Tofolo *et al*. 2011). Since nocturnal activity was not considered in this study and resource availability can change at night, we do not know how our characterization of *E. vizottoi*'s diet would differ if the species' foraging activity were observed for a full 24 hours. Richard *et al*. (2004) and Passera *et al*. (1994), who respectively investigated *E. tuberculatum*'s and *E. ruidum*'s foraging activity, observed that both species' activity was linked with the nocturnal secretion rhythm of nectaries.

Foragers of *E. vizottoi* have never been observed to recruit other foragers, and they hunt individually, as do *E. tuberculatum*, *E. opaciventre*, and *E. brunneum* (Overal 1986; Wheeler 1986; Valenzuela-González *et al*.1995; Pie 2004; Gomes *et al*. 2009). In contrast, *E. ruidum* has been found to lay chemical trails to initiate mass recruitment to rich or difficult-to-harvest food resources and to use graded recruitment as a strategy to obtain food (Pratt 1989; Schatz *et al*. 1997), even though some past reports state that this species hunts individually. Ectatomminae foragers may use a wide variety of strategies to obtain food while hunting individually; they may show no cooperation while searching for and collecting food or demonstrate varying degrees of cooperation, with different levels of communication and recruitment taking place among nestmates. Furthermore, diets can vary widely among species and can include seeds, fruit, living prey, and/or insect secretions (Hölldobler & Wilson 1990; Medeiros & Oliveira 2009; Tofolo *et al*. 2011).

Our results show that *E. vizottoi* has foraging strategies similar to those of other species in *Ectatomma*. We highlight the finding that, in spite of their low efficiency indices, colonies adopted strategies that allowed them to successfully obtain food resources while avoiding adverse conditions, including preying on other ant species more frequently. This foraging strategy may arise because resource diversity in the environment is limited (Tofolo *et al*. 2011) or because, regardless of resource availability, *E. vizottoi* preferentially preys on other invertebrates and especially other ant species (Lachaud *et al*. 1996).

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