

Research article

Patterns in foraging and nesting ecology in the neotropical ant, *Gnamptogenys moelleri* (Formicidae, Ponerinae)

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Summary. This study provides quantitative field data on the natural history and foraging behaviour of the Neotropical bromeliad-nesting ant *Gnamptogenys moelleri* (Ponerinae) in a sandy plain forest in Southeast Brazil. The ant nested on different bromeliad species and the nests were more frequently found in bigger bromeliads. The species used a wide array of invertebrates in its diet, hunting for live prey and scavenging the majority of the items from dead animals. The food items varied greatly in size (1 to 26 mm). Hunting was always performed by solitary workers. Retrieving was performed by solitary workers (small items), or by a group of 3 to 12 workers recruited to the food source (large items). Almost all *G. moelleri* foraging activity was restricted to the nest bromeliad. In the warm period more ants left the nest to forage, and foraging trips achieved greater distances compared to the cool season. Trap data revealed that overall availability of arthropod prey is higher in the summer than in the winter. The opportunism in nest site use and in foraging behaviour, the small foraging area, as well as the seasonal differences in foraging activity are discussed and compared with other tropical ants.

Key words: ants, foraging, *Gnamptogenys*, nesting, Ponerinae.

Introduction

Because ants employ a variety of foraging strategies and foragers usually depart from a fixed nest location, they are excellent models to test ecological and evolutionary hypotheses about foraging behaviour (Carroll and Janzen, 1973). However, to fully understand an ant colony foraging system

one must determine both the individual and social components of the foraging behaviour, and the ecological setting in which the colony occurs (Traniello, 1989). Therefore, the development of models and hypotheses about ant foraging strategies is constrained by the small amount of quantitative data on foraging behaviour in different species (Duncan and Crewe, 1994). In the Neotropics, where ant abundance and number of species are remarkable, data on basic ecological attributes of ants are still scarce.

Ants in the subfamily Ponerinae are considered a phylogenetically basal group because they have retained a large proportion of morphological and behavioural ancestral traits, such as small colonies, simple nests, and solitary foraging (Peeters, 1997). Most ponerine ants nest on the ground – some species are able only to make limited modifications in pre-existing nest structures while others invest much labour in building permanent nests (Hölldobler and Wilson, 1990). Ponerine ants may forage on the ground and on plant foliage, searching for solid and liquid food (Carroll and Janzen, 1973). Because all ponerine species are armed with a sting, they are generally regarded as predatory ants. However, some species also scavenge for dead arthropods, and may feed on extrafloral nectar, Homoptera honeydew, secretion of lepidopteran larvae, as well as fruits and seeds (Carroll and Janzen, 1973; DeVries, 1991; Oliveira and Brandão, 1991; Dejean and Lachaud, 1994; Pizo and Oliveira, 1998; Del-Claro and Oliveira, 1999). Many ponerine species are opportunistic in their choice of food items, while others are very prey-specific (Peeters and Crewe, 1987; Fresneau, 1985; Pratt, 1989; Brown, 1992; Leal and Oliveira, 1995; Freitas, 1995; Ehmer and Hölldobler, 1995; Fourcassié and Oliveira, 2002). Ponerine ants also vary widely in the strategy used to forage, ranging from solitary hunting without any co-operation during search and food retrieval, to different levels of cooperative foraging mediated by varying degrees of recruitment communication between nestmates (Peeters and Crewe,

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1987; Hölldobler and Wilson, 1990). Moreover, variation in biotic (e.g., competition, natural enemies) and abiotic (e.g., temperature, humidity) factors are also likely to affect ant foraging activity both daily and seasonally (Carroll and Janzen, 1973; Traniello, 1989; Orivel and Dejean, 2001; Hahn and Wheeler, 2002).

Ants in the genus *Gnamptogenys* are widespread in the Oriental, Indo-Australian and Neotropical regions, with almost 100 species described (Lattke, 1995; Bolton, 1995). *Gnamptogenys* is phylogenetically close to the genera *Ectatomma* and *Rhytidoponera*, all belonging to the tribe Ectatommini, a derived taxon in the Ponerinae (Lattke, 1994; Keller, 2000). Most *Gnamptogenys* species are considered rare and cryptic, and studies on their behaviour and ecology are scarce. Pratt (1994) reported that *G. horni* feeds on a wide variety of ants and other arthropods, and that workers present age-based division of labour. *Gnamptogenys menadensis*, an arboreal species with differentiated queens and gamergates, forages on shrubs and trees, and reproduces by colony fragmentation (Gobin et al., 1998a, b). Additionally, *G. menadensis* uses chemical trails during homing, and also recruits nestmates to dense clusters of prey (Gobin et al., 1998b; Johnson et al., 2003).

This study provides quantitative and qualitative field data on the natural history and foraging behaviour of the small (ca. 0.5 cm), bromeliad-nesting ant *G. moelleri*. This Neotropical species is considered an epigeic forager in lowland forested areas (Lattke, 1995). The following aspects were studied: (1) colony demography, (2) nesting ecology, (3) diet, and (4) spatial foraging range and activity in two seasons.

Material and methods

Study Site

Fieldwork was carried out in the sandy plain forest ("restinga" forest) of the Parque Estadual da Ilha do Cardoso (25°03'S; 47°53'W), a 22500 ha island located off the coast of São Paulo State, SE Brazil (0–800 m a.s.l.). The area has an open canopy formed by 5–15 m tall trees growing on poor sandy soil, and abundant bromeliads growing both on the ground and as epiphytes (Oliveira-Filho and Fontes, 2000; Barros et al., 1991). Mean annual temperature and rainfall are 20.9°C and 3000 mm, respectively. There is a marked difference between two seasons: a cool and relatively dry period (winter) from April to August (mean temperature 13°C, mean rainfall 500 mm) and a warm and rainy period (summer) from September to March (mean temperature 32°C, mean rainfall 1800 mm). Daylight periods are approximately from 6:00 to 18:00 h during the winter, and from 6:00 to 19:00 h during the summer.

Demography, and use of bromeliads for nesting

Initial observations showed that *G. moelleri* nests on both ground and epiphytic bromeliad species. By following loaded workers attracted to baits, several bromeliads containing *G. moelleri* colonies were marked in the sandy forest. Nine of these colonies were chosen for demographic data. Five colonies were collected during the winter and four during the summer. Ant voucher specimens are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil. To investigate whether the characteristics of the bromeliads used as nests

by *G. moelleri* are different from the general bromeliads available in the sandy plain forest, the following approach was undertaken in February 2002: along a ca. 2000 m-transect all bromeliads close to the transect (ca. 1.5 m on each side) were inspected for the presence of ant colonies. Nest location was determined by placing a bait (0.5 cm pellet of tuna on a 5 × 5 cm filter paper) on each bromeliad, and following loaded workers. A total of 52 bromeliads containing a *G. moelleri* colony were found. Additionally, 200 points were established (ca. 10 m apart) in the same transect, and the closest bromeliad to each point was tagged and used as controls to be compared with the bromeliads with ant nest. For each bromeliad (with and without an ant colony), the taxonomic identity, number of leaves, length and diameter of the rosette, and the number of bridges formed with neighbouring foliage were recorded.

Surveys of food items

The food items retrieved by three *G. moelleri* colonies (#5, #25, #26) were surveyed in December 2001. Several observation sessions were carried out between 6:00 and 22:00 h, resulting in a total of 90 h of observations of the three colonies. Food items were removed from the mandibles of returning foragers, totalling 104 collected items. The number of foragers retrieving items was also recorded. Food items were conserved in 70% ethanol and identified at the family level in most cases. The length of the items (at the longest anterior-posterior axis) was measured to the nearest 0.01 mm. The items were kept in an oven at 35°C for 24 h, and their dry weights were determined to the nearest 0.01 mg.

Spatial foraging range

To determine the foraging range of *G. moelleri* workers, three colonies (#5, #25, #26) were observed in both seasons (July and December 2001). In each season, each colony was observed continuously during 5 h (18:00–23:00 h) and all workers leaving the nest were followed. The foraging path – bromeliad leaves, nearby trees and shrubs, and ground – of each worker was recorded. The time duration of each foraging trip and the maximal distance from the nest reached by workers were also recorded.

Seasonal variation in the availability of potential arthropod prey was evaluated with sticky strip traps placed on the vegetation in July and December 2001. The trap was a 21 × 16 cm white cardboard with a thin layer of Tanglefoot® (Tanglefoot Co., Grand Rapids, Michigan). In each period 20 traps, 10 m apart from each other, were left on the foliage (ca. 0.5 m high) for 24 h.

Statistical analyses

The frequency distribution of the bromeliad species containing *G. moelleri* colonies was compared with the general distribution of bromeliads in the forest using a contingency G test. The characteristics (leaf number, length and diameter of the rosette, and the number of bridges formed with nearby vegetation) of bromeliads used as nest by *G. moelleri* were compared with the traits of the general bromeliad community by Mann-Whitney U tests, using Bonferroni correction. The probability of a worker to recruit nestmates as a function of the food item's dry weight was analysed with a logistic regression model (Hosmer and Lemeshow, 1989; Hardy and Field, 1998). Spearman's coefficient was used to express the correlation between number of workers carrying a food item and the item dry weight. Foraging activity in the summer and winter was compared by paired t tests. Maximal distances achieved by foragers and duration of foraging trips in each season were analysed by two-factor analyses of variance (season and colony as factors) after log transformation of the data. The mean number of arthropods captured per trap in each season was compared by a t test.

Results

Demography and use of bromeliads as nest

The demographic data of nine colonies of *G. moelleri* collected in bromeliads is presented in Table 1. Each of six colonies contained one queen, and three colonies were queenless. In the summer the colonies had more larvae and pupae, while the presence of male and female alates was more common in the winter (Table 1).

Gnamptogenys moelleri colonies were found in four bromeliad species (Table 2). The frequency distribution of the species used did not differ from the distribution of eight bromeliad species growing in the sandy forest (Table 2; $G = 8.41$, d.f. = 7, $p = 0.30$). *Quesnelia arvensis*, the most common bromeliad used by ants as nest, was also the most frequent species in the forest. Compared with the general bromeliad community of the study area, the bromeliads with *G. moelleri* nests had higher number of leaves ($U = 2776$; $n_1 = 200$; $n_2 = 52$; $p < 0.0001$), higher number of bridges formed with nearby vegetation ($U = 3320$; $n_1 = 200$; $n_2 = 52$; $p < 0.0001$), higher rosette diameter ($U = 2782$; $n_1 = 200$; $n_2 = 52$; $p < 0.0001$), and higher rosette length ($U = 2722$; $n_1 = 200$; $n_2 = 52$; $p < 0.0001$) (Fig. 1).

Diet

Gnamptogenys moelleri workers are opportunistic foragers, including a wide array of invertebrates in their diet (Table 3). Even though workers hunted for live prey, the vast majority of the items were scavenged dead animals. Workers were also observed feeding on extrafloral nectar on foliage ($n = 3$ observations). The food items used varied greatly in weight (Fig. 2), ranging from small flies (0.1 mg, 2 mm in length) to large bugs (100 mg, 20 mm in length). Hunting was always performed by solitary workers. Retrieving was performed by solitary workers or by a group of nestmates (3–12 ants) recruited to the food source. While small items were retrieved by solitary workers, large items were retrieved in group. The probability of a worker to recruit nestmates increased with load weight (Fig. 3A). Additionally, the number of workers carrying the item was positively

Table 2. Percent distribution of bromeliad species in the sandy plain forest of Ilha do Cardoso, Southeast Brazil. Data represent the general bromeliad community, and the bromeliads containing a *Gnamptogenys moelleri* colony.

Bromeliad species	Ground or Epiphyte	Percent of bromeliads	
		With ant colony (%) (n = 52)	General community (%) (n = 200)
<i>Quesnelia arvensis</i>	G	83	60
<i>Vriesea phillippocoburgii</i>	E	10	12
<i>Vriesea</i> sp. 1	E	6	12
<i>Aechmea nudicaulis</i>	E	2	6
<i>Nidularium</i> sp.	G	0	2
<i>Vriesea</i> sp. 2	E	0	1
Undetermined 1	G, E	0	6
Undetermined 2	G	0	2

correlated with item weight ($r_s = 0.643$; $n = 104$; $p < 0.0001$; Fig. 3B).

Spatial foraging range in two seasons

Almost all foraging activity of *G. moelleri* is restricted to the nest bromeliad. During the winter, all foragers searched for food on the bromeliad leaves. In the summer some ants hunted also on the ground and on nearby shrubs and trees, but the vast majority used just the bromeliad leaves (Table 4). Although the number of ants leaving the nest were higher in the summer than in the winter, the percentage of successful foragers retrieving food items did not differ between seasons (Table 4). Foraging distances also increased in the summer. The duration of foraging trips, however, was higher in the cold than in the warm season (Table 4). During the winter foragers frequently remained motionless on leaves for some time (ca. 1 to 3 minutes), a behaviour never seen in the summer. Neither foraging distance ($F_{2,415} = 1.16$, $p = 0.31$) nor duration of trips ($F_{2,415} = 2.69$, $p = 0.07$) varied significantly

Table 1. Composition of five colonies of *Gnamptogenys moelleri* collected in the cool season (June and July), and four colonies collected in the warm season (February and March) in the sandy plain forest of Ilha do Cardoso, Southeast Brazil

Month of collection	Colony code	No. of queens	No. of eggs	No. of larvae	No. of pupae	No. of female alates	No. of male alates	No. or workers
June	#11	1	1	1	0	0	0	12
July	#12	1	0	5	0	35	0	65
July	#13	1	10	2	0	0	27	120
July	#27	0	0	0	0	0	5	46
July	#28	1	8	4	0	37	0	186
March	#6	0	0	1	18	0	11	58
February	#40	0	2	101	42	0	0	102
February	#42	1	0	41	14	0	0	123
February	#48	1	22	31	26	0	0	53

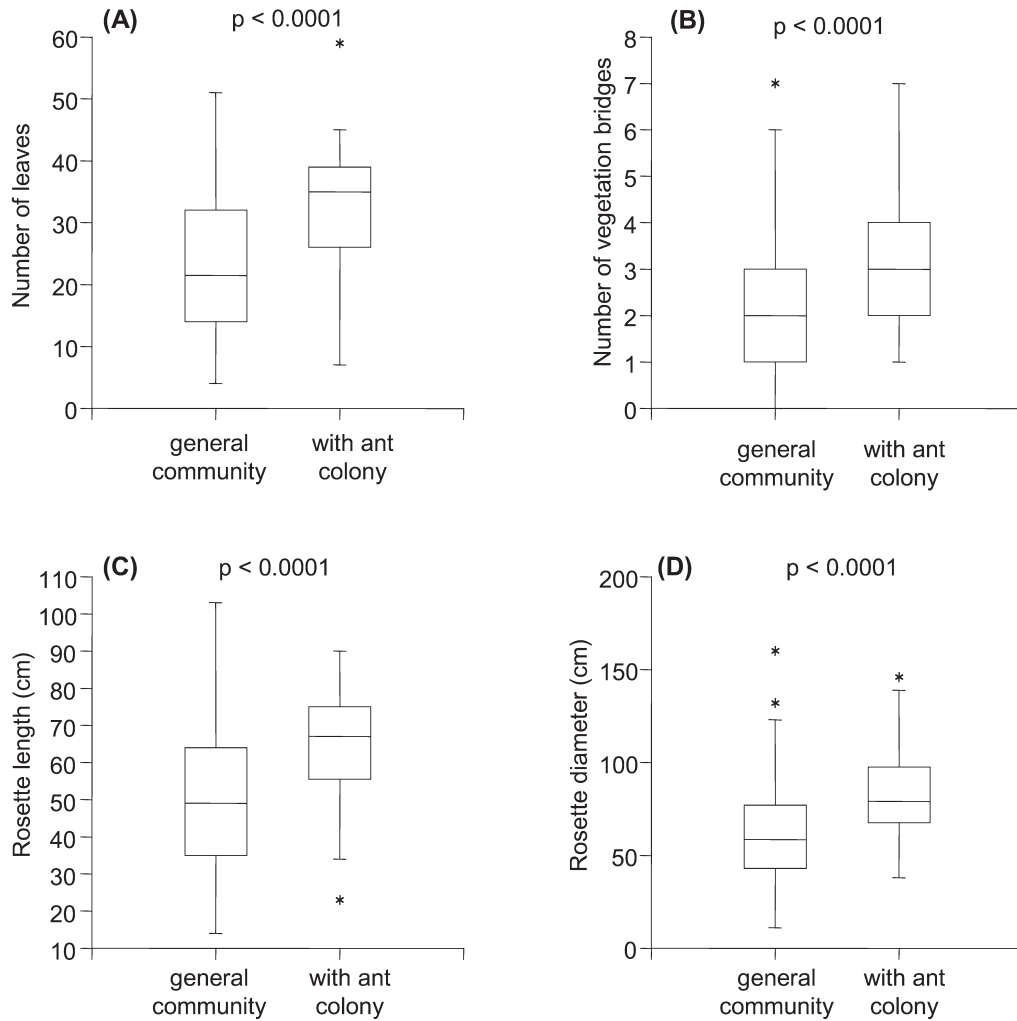


Figure 1. Characteristics of bromeliads used as nests by *Gnamptogenys moelleri*, and of the general bromeliad community in the sandy plain forest of Ilha do Cardoso, Southeast Brazil. (A) number of leaves, (B) number of bridges formed with nearby trees and shrubs, (C) rosette length and (D) rosette diameter. The horizontal line inside the box represents the median and the horizontal ends of the box represent the 25th and 75th percentiles. Asterisks represent outside values. *p* shows the probability of Mann-Whitney U tests.

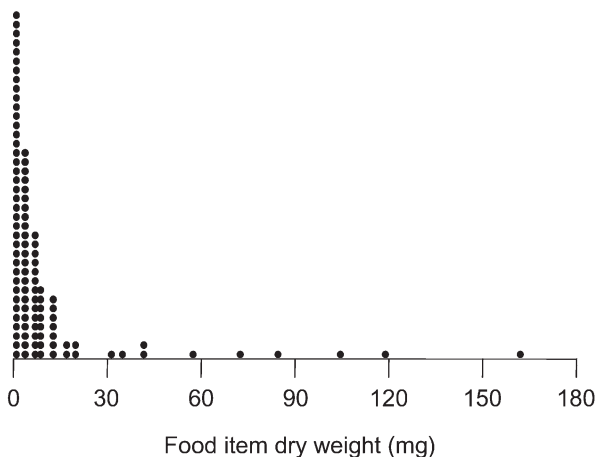


Figure 2. Dot density showing the frequency of food items ($n = 104$) observed across the range of the dry weight. Food items were retrieved by *Gnamptogenys moelleri* in the sandy plain forest of Ilha do Cardoso, Southeast Brazil.

among colonies. The data from the traps revealed a marked seasonal difference in the overall availability of arthropods in the forest, with many more arthropods being captured per trap in the summer than in the winter (Table 4).

Discussion

The occurrence of arboreal nests is rare in ponerine ants, and just a few species, such as *Gnamptogenys menadensis*, *Pachycondyla goeldii*, *P. villosa*, *P. inversa*, *P. luteola*, and *Platythyrea conradti* nest frequently on vegetation (Dejean and Olmsted, 1997; Peeters, 1997; Gobin et al., 1998a; Lucas et al., 2002). Bromeliads are among the most frequent sites used as nest by arboreal ants in the Neotropics (Dejean et al., 1995; Blüthgen et al., 2000; Camargo, 2002). In phytotelm bromeliads there are basically two kinds of animal assemblages: (1) aquatic animals in the accumulated rainwater, and

Table 3. Food items retrieved by *Gnamptogenys moelleri* foragers in the sandy plain forest of Ilha do Cardoso, Southeast Brazil. Data result from 90 h of observation of three colonies.

Taxonomic identity	No. of items (%) n = 104	No. of live prey
ANNELIDA		
Oligochaeta	3 (2.9)	1
MYRIAPODA		
Diplopoda	1 (1.0)	
INSECTA		
Orthoptera		
Acrididae	3 (2.9)	
Tettigoniidae	2 (1.9)	
Blattidae	1 (1.0)	
Isoptera		
Rhinotermitidae		
alate	20 (19.2)	
worker	1 (1.0)	1
Homoptera		
Cercopidae	1 (1.0)	
Heteroptera		
Coreidae	1 (1.0)	
Pentatomidae	2 (1.9)	
Reduviidae	2 (1.9)	
Coleoptera		
Crysolimelidae	6 (5.8)	
Curculionidae	2 (1.9)	1
Elateridae	3 (2.9)	
Lampyridae	4 (3.8)	
Diptera		
Culicidae	26 (25.0)	
Tabanidae	3 (2.9)	
Lepidoptera		
adult	1 (1.0)	
larvae	6 (5.8)	2
Hymenoptera		
Sphecidae	1 (1.0)	
Formicidae		
worker	2 (1.9)	1
alate	13 (12.5)	

(2) non-aquatic ones, like ant colonies, which live in the drier parts of the plant (see Dejean and Olmsted, 1997). These phytotelm bromeliads are different from myrmecophytic species, which have special morphological modifications to house ant colonies (see Huxley, 1980). In myrmecophytic bromeliads the association with ants is species-specific, while non-myrmecophytic bromeliads may host colonies of many ant species (Blüthgen et al., 2000). *Gnamptogenys moelleri* confirms this pattern by opportunistically using different bromeliad species in the same frequency that the plants occur in the forest (Table 2). Additionally, other ant species such as *Odontomachus hastatus*, *Dolichoderus attenaboides*, *Camponotus* sp. and *Crematogaster* sp. may also nest in bromeliads in the study area (Camargo, 2002). Despite the random use of bromeliad species, the characteristics of the plants used as nest by *G. moelleri* did differ from the general bromeliad community (Fig. 1), and nests were more frequently found in larger bromeliads (i.e., more leaves

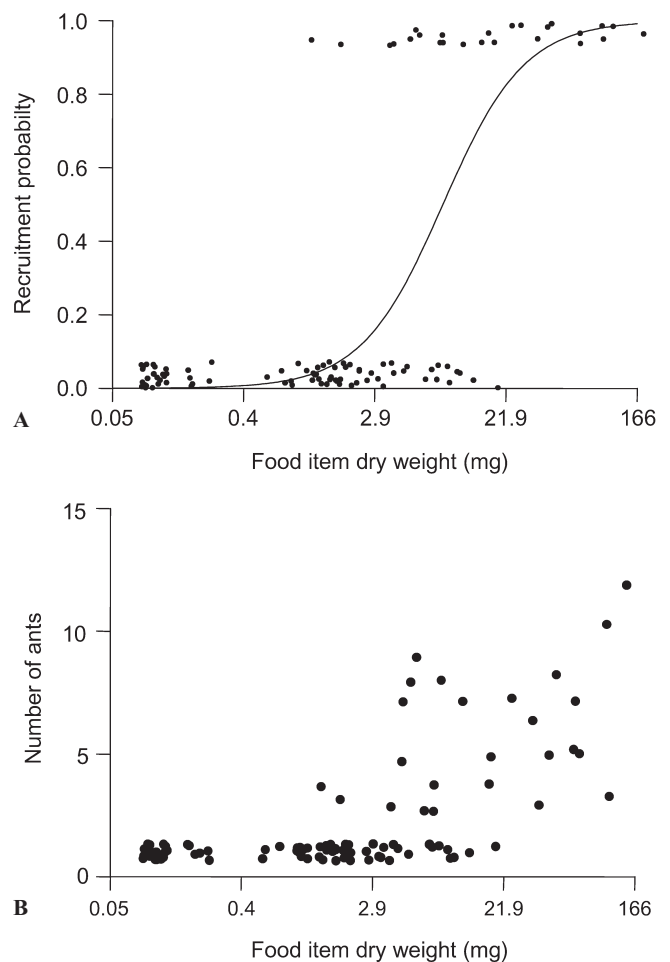


Figure 3. *Gnamptogenys moelleri* recruitment behaviour during foraging activity in the sandy plain forest of Ilha do Cardoso, Southeast Brazil. (A) Probability of a forager to recruit nestmates as a function of food item dry weight (data points are slightly displaced from 0 or from 1 for visual clarity). Food item weight was log transformed. Values of the logistic regression model are: constant = -3.352, parameter = 3.655; $G = 58.478$, number of observations = 104, negative responses = 79, positive responses = 25, $p < 0.001$, odds ratio = 38.678. (B) Correlation between number of recruited foragers and dry weight of food item ($n = 104$). Food item weight was log transformed and data points are slightly randomly displaced to avoid overlaps.

and larger rosette). What are the possible advantages to the colony associated with this pattern? First, one may suppose that colony growth could be limited by nest space, as has already been reported in myrmecophytic plants (Fonseca, 1993). However, this is unlikely to be relevant for *G. moelleri* because colonies occupy the base of just 1–3 leaves of the entire bromeliad, suggesting that the colony is free to grow larger. Second, given that the vast majority of foraging trips occur in the nest bromeliad, larger plants represent increased foraging area and more potential prey for the ant colony. Additionally, *G. moelleri* nests were more common in bromeliads with higher number of bridges with nearby vegetation, which is certainly important for expanding the colony foraging area onto nearby trees, shrubs, and other bromeliads.

Table 4. Seasonality in the foraging ecology of *Gnamptogenys moelleri* in the sandy plain forest of Ilha do Cardoso, Southeast Brazil. Data are based on three colonies (#5, #25, #26) observed in July and December 2001. Numbers of foragers seen in each substrate are given between brackets. Key to foraging substrates: NB = nest bromeliad; T = trees; G = ground. Values are means \pm S.D.; ranges are given between parentheses for both periods.

Variable	Winter	Summer	Significance
Type of foraging substrate			
colony #5	NB [49]	NB [89], T [4]	–
colony #25	NB [26]	NB [114], T [7]	–
colony #26	NB [21]	NB [100], T [3], G [6]	–
Ants leaving nest (n = 3 colonies)	32.0 \pm 14.9 (21–49)	107.7 \pm 14.0 (93–121)	p = 0.042 (t = 4.74; d.f. = 2)
Foragers retrieving food (%) (n = 3 colonies)	1.9 \pm 1.9 (0–3.8)	5.2 \pm 1.1 (4.2–6.4)	p = 0.177 (t = 2.05; d.f. = 2)
Foraging distance (cm) (n _{summer} = 323, n _{winter} = 96)	34.6 \pm 11.5 (12–53)	44.9 \pm 22.7 (10–180)	p < 0.001 (F _{1,415} = 21.04)
Duration of foraging trip (sec) (n _{summer} = 323, n _{winter} = 96)	137 \pm 113 (12–510)	96 \pm 133 (15–1132)	p < 0.001 (F _{1,415} = 19.10)
No. of arthropod prey per trap (n = 20 traps)	1.8 \pm 1.3 (0–4)	4.6 \pm 3.2 (0–14)	p = 0.001 (t = 3.70; d.f. = 38)

Studying the Australian ponerine ant *Rhytidoponera metallica*, Thomas (2002) demonstrated that colony growth is limited by the size of the rock cavities used as nest site, and that workers are capable of recognising large rocks to where colonies frequently migrate in the field. In our study it is not possible to know if the colonies are capable to actively recognise bigger bromeliads. However, it is conceivable that colonies frequently migrate in the field. On several occasions tagged bromeliads with a *G. moelleri* colony were found without the ants in succeeding months. In addition, frequent nest migrations have already been observed in other *Gnamptogenys* species (Giraud et al., 2000; Gobin et al., 1998a). Thus, colony migration to more favourable bromeliads may explain why ant-occupied plants are larger than unoccupied plants. However, there are two other possible explanations for this pattern. First, colonies may experience decreased survival in small bromeliads compared to large ones. Second, plants housing an ant colony may grow more vigorously than unoccupied plants because workers may deter defoliators and/or provide nutrients to the plant due to accumulation of organic matter such as faeces, prey remains and dead individuals (see Huxley, 1980).

Gnamptogenys moelleri foragers collect a wide array of invertebrates, including live prey, dead animals, as well as extrafloral nectar. The taxonomic diversity of the food in *G. moelleri*'s diet is similar to that recorded for other ponerine species living in tropical forests (see Introduction). However, this pattern contrasts with other *Gnamptogenys* species exhibiting specialisation on certain types of prey such as ants (Pratt, 1994), and millipedes (Brown, 1992). In addition to the food items recorded in this study, *G. moelleri* also collects fleshy seeds and fruits. Passos and Oliveira (2002, 2003) reported several *G. moelleri* foragers retrieving fallen fleshy diaspores (arilate seeds and fruits) of different plant species in the same sandy forest. Many ponerine ants complement their diets with fleshy portions of seeds and fruits, and this behaviour has also been reported in other Neotropical

Gnamptogenys species (Pizo and Oliveira, 1998, 2000; Guimarães and Cogni, 2002).

Foraging strategies in the Ponerinae do not reflect phylogenetic relationship and are likely the result from unique selective pressures faced by each species (Peeters and Crewe, 1987; Hölldobler and Wilson, 1990; Peeters, 1997). One interesting pattern in the foraging strategy of *G. moelleri* is that the vast majority of food items retrieved was scavenged from dead invertebrates. Thus, since there is no cost associated with subduing live prey or with loosing prey due to escape, the foraging task can be performed by just one ant. Moreover, retrieved food items are widely variable in size (Fig. 2), and recruitment of nestmates allows the small workers to retrieve large food items. Therefore, recruitment communication widens the size range of food items available for *G. moelleri* colonies (see Traniello, 1987). Another ecological factor that may have shaped *G. moelleri*'s recruitment behaviour is the particular architecture of its foraging environment (see also Johnson et al., 2003). Ants foraging exclusively on vegetation may have a high probability of encountering another forager on the return trip, due to the limited number of primary branch routes leading to the nest. Indeed, Johnson et al. (2003) suggested that habitat architecture is the main factor shaping recruitment behaviour in arboreal *G. menadensis*. However, unlike *G. moelleri* whose foraging range is limited primarily to the nest bromeliad, *G. menadensis* colonies maintain a high proportion of foragers out on branches and recruit to dense accumulations of termite prey, regardless of distance (Johnson et al., 2003). A detailed study about recruitment behaviour during foraging in *G. moelleri* is reported elsewhere (Cogni and Oliveira, submitted).

G. moelleri's foraging activity varies markedly between seasons. In the summer more ants leave the nest to forage, and foragers go to greater distances than in the cold season (Table 4). Seasonal variation in foraging range has already been reported in other tropical ponerines, such as *Brachyponera senaarensis*, *Pachycondyla marginata*, and *P. striata*

(Dejean and Lachaud, 1994; Leal and Oliveira, 1995; Medeiros, 1997). More intense foraging activity by *G. moelleri* in the warm season corresponds with the period of greater quantity of brood in the colonies (Table 1), and increased abundance of arthropod prey in the environment (Table 4).

In conclusion, *G. moelleri* presented an opportunistic foraging behaviour, with a flexible diet that includes live and dead invertebrates, as well as nectar. Additionally, recruitment of nestmates allows the workers to retrieve large food items, widening the size range of the items included in the diet. Foraging activity showed a marked variation between seasons, which are associated with physical factors, and food availability. The species is also opportunistic in the use of bromeliad species for nesting. *Gnamptogenys moelleri* tends to nest preferably in large bromeliads, where most of the foraging activity takes place. This study illustrates how quantitative data on the natural history, ecology, and behaviour of a social insect species can link ecological factors and foraging strategies, thus helping our understanding of the patterns observed.

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References

- Barros, F., M.M.R.F. Melo, S.A.C. Chiea, M. Kirizawa, M.G.L. Wanderley and S.L. Jung-Mendaçolli, 1991. *Flora fanerogâmica da Ilha do Cardoso, I*. Instituto de Botânica, São Paulo. pp. 184.
- Blüthgen, N., M. Verhaagh, W. Goitia and N. Blüthgen, 2000. Ant nests in tank bromeliads – an example of non-specific interaction. *Insect. Soc.* 47: 313–316.
- Bolton, B., 1995. A taxonomic and zoogeographical census of the extant ant taxa (Hymenoptera: Formicidae). *J. Nat. Hist.* 29: 1037–1056.
- Brown, W.L., 1992. Two new species of *Gnamptogenys* and an account of millipede predation by one of them. *Psyche* 99: 275–289.
- Camargo, R.X., 2002. *Ecologia e comportamento da formiga arbórea Odontomachus hastatus (Hymenoptera: Formicidae: Ponerinae)*. Master thesis, Universidade Estadual de Campinas, Campinas.
- Carroll, C.R. and D.H. Janzen, 1973. Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.* 4: 231–257.
- Dejean, A. and J.P. Lachaud, 1994. Ecology and behavior of the seed-eating ponerine ant *Brachyponera senaarensis* (Mayr). *Insect. Soc.* 41: 191–210.
- Dejean, A. and I. Olmsted, 1997. Ecological studies on *Aechmea bracteata* (Swartz) (Bromeliaceae). *J. Nat. Hist.* 31: 1313–1334.
- Dejean, A., I. Olmsted and R.R. Snelling, 1995. Tree-epiphyte-ant relationships in the low inundated forest of Sian Ka'an Biosphere Reserve, Quintana Roo, Mexico. *Biotropica* 27: 57–70.
- Del-Claro, K. and P.S. Oliveira, 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.
- DeVries, P.J., 1991. Mutualism between *Thisbe irenea* butterflies and ants, and the role of ant ecology in the evolution of larval-ant associations. *Biol. J. Linn. Soc.* 43: 179–195.
- Duncan, F.D. and R.M. Crewe, 1994. Field study on the foraging characteristics of a ponerine ant, *Hagensia havilandi* Forel. *Insect. Soc.* 41: 85–98.
- Ehmer, B. and B. Hölldobler, 1995. Foraging behavior of *Odontomachus bauri* on Barro Colorado Island, Panama. *Psyche* 102: 215–224.
- Freitas, A.V.L., 1995. Nest relocation and prey specialization in the ant *Leptogenys propefalcigera* Roger (Formicidae: Ponerinae) in an urban area in southeastern Brazil. *Insect. Soc.* 42: 453–456.
- Fresneau, D., 1985. Individual foraging and path fidelity in a ponerine ant. *Insect. Soc.* 32: 109–116.
- Fonseca, C.R., 1993. Nesting space limits colony size of the plant-ant *Pseudomyrmex concolor*. *Oikos* 67: 473–482.
- Fourcassié, V. and P.S. Oliveira, 2002. Foraging ecology of the giant Amazonian ant *Dinoponera gigantea* (Hymenoptera, Formicidae, Ponerinae): activity schedule, diet, and spatial foraging patterns. *J. Nat. Hist.* 36: 2211–2227.
- Giraud, T., R. Blatrix, C. Poteaux, M. Solignac and P. Jaisson, 2000. Population structure and mating biology of the polygynous ponerine ant *Gnamptogenys striatula* in Brazil. *Mol. Ecol.* 9: 1835–1841.
- Gobin, B., C. Peeters and J. Billen, 1998a. Colony reproduction and arboreal life in the ponerine ant *Gnamptogenys menadensis* (Hymenoptera: Formicidae). *Neth. J. Zool.* 48: 53–63.
- Gobin, B., C. Peeters, J. Billen and E.D. Morgan, 1998b. Interpecific trail following and commensalism between the ponerine ant *Gnamptogenys menadensis* and the formicine ant *Polyrhachis rufipes*. *J. Insect Behav.* 11: 361–369.
- Gobin, B., J. Billen and C. Peeters, 2001. Dominance interactions regulate worker mating in the polygynous ponerine ant *Gnamptogenys menadensis*. *Ethology* 107: 495–508.
- Guimarães, P.R. and R. Cogni, 2002. Seed cleaning of *Cupania vernalis* (Sapindaceae) by ants: edge effect in a highland forest in south-east Brazil. *J. Trop. Ecol.* 18: 303–307.
- Hahn, D.A. and D.E. Wheeler, 2002. Seasonal foraging activity and bait preferences of ants on Barro Colorado Island, Panama. *Biotropica* 34: 348–356.
- Hardy, I.C.W. and S.A. Field, 1998. Logistic analysis of animal contests. *Anim. Behav.* 56: 787–792.
- Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. Harvard University Press, Cambridge, Mass. pp. 732.
- Hosmer, D.W. and S. Lemeshow, 1989. *Applied Logistic Regression*. John Wiley & Sons, New York. pp. 307.
- Huxley, C.R., 1980. Symbiosis between ants and epiphytes. *Biol. Rev.* 55: 321–340.
- Johnson, C.A., E. Lommelen, D. Allard and B. Gobin, 2003. The emergence of collective foraging in the arboreal *Gnamptogenys menadensis* (Hymenoptera: Formicidae). *Naturwissenschaften* 90: 332–336.
- Keller, R.A., 2000. Cladistics of the tribe Ectatommini (Hymenoptera: Formicidae): a reappraisal. *Insect Syst. Evol.* 31: 59–69.
- Lattke, J.E., 1994. Phylogenetic relationships and classification of Ectatommine ants (Hymenoptera: Formicidae). *Entomol. Scand.* 25: 105–119.
- Lattke, J.E., 1995. Revision of the ant genus *Gnamptogenys* in the New World (Hymenoptera: Formicidae). *J. Hym. Res.* 4: 137–193.
- Leal, I.R. and P.S. Oliveira, 1995. Behavioral ecology of the Neotropical termite-hunting ant *Pachycondyla (=Termitopone) marginata*: colony founding, group raiding and migratory patterns. *Behav. Ecol. Sociobiol.* 37: 373–383.
- Lucas, C., D. Fresneau, K. Kolmer, J. Heinze, J.H.C. Delabie and D.B. Pho, 2002. A multidisciplinary approach to discriminating different taxa in the species complex *Pachycondyla villosa* (Formicidae). *Biol. J. Linn. Soc.* 75: 249–259.

- Medeiros, F.N.S., 1997. *Ecologia comportamental da formiga Pachycondyla striata Fr. Smith (Formicidae: Ponerinae) em uma floresta do Sudeste do Brasil*. Master thesis, Universidade Estadual de Campinas, Campinas.
- Oliveira, P.S. and C.R.F. Brandão, 1991. The ant community associated with extrafloral nectaries in the Brazilian cerrados. In: *Ant-Plant Interactions* (D.F. Cutler and C.R. Huxley, Eds.), Oxford University Press, Oxford. pp. 198–212.
- Oliveira-Filho, A.T. and M.A.L. Fontes, 2000. Patterns of floristic differentiation among Atlantic Forest in Southeastern Brazil and the influence of climate. *Biotropica* 32: 793–810.
- Orivel, J. and A. Dejean, 2001. Ant activity rhythms in a pioneer vegetal formation of French Guiana (Hymenoptera: Formicidae). *Sociobiology* 38: 1–12.
- Passos, L. and P.S. Oliveira, 2002. Ants affect the distribution and performance of seedlings of *Clusia criuva*, a primarily bird-dispersed rain forest tree. *J. Ecol.* 90: 517–528.
- Passos, L. and P.S. Oliveira, 2003. Interactions between ants, fruits, and seeds in a restinga forest in south-eastern Brazil. *J. Trop. Ecol.* 19: 261–270.
- Peeters, C., 1997. Morphologically 'primitive' ants: comparative review of social characters, and the importance of queen-worker dimorphism. In: *The Evolution of Social Behavior in Insects and Arachnids* (J.C. Choe and B.J. Crespi, Eds.), Cambridge University Press, Cambridge. pp. 372–391.
- Peeters, C. and R. Crewe, 1987. Foraging and recruitment in ponerine ants: solitary hunting in the queenless *Ophthalmopone berthoudi* (Hymenoptera: Formicidae). *Psyche* 94: 201–214.
- Pizo, M.A. and P.S. Oliveira, 1998. Interaction between ants and seeds of a nonmyrmecochorous Neotropical tree, *Cabrlea canjerana* (Meliaceae), in the Atlantic forest of southeast Brazil. *Amer. J. Bot.* 85: 669–674.
- Pizo, M.A. and P.S. Oliveira, 2000. The use of fruits and seeds by ants in the Atlantic Forest of Southeast Brazil. *Biotropica* 32: 851–861.
- 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: Ponerine). *Insect. Soc.* 41: 255–262.
- Thomas, M.L., 2002. Nest site selection and longevity in the ponerine ant *Rhytidoponera metallica* (Hymenoptera, Formicidae). *Insect. Soc.* 49: 147–152.
- Traniello, J.F.A. 1987. Comparative foraging ecology of north temperate ants: the role of worker size and cooperative foraging in prey selection. *Insect. Soc.* 34: 118–130.
- Traniello, J.F.A., 1989. Foraging strategies of ants. *Annu. Rev. Entomol.* 34: 191–210.



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