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ECOLOGIA DO FORRAGEAMENTO E RECRUTAMENTO NA FORMIGA *GNAMPTOGENYS MOELLERI* (FOREL) (PONERINAE: ECTATOMMINI)

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INTRODUÇÃO GERAL

Formigas (Hymenoptera: Formicidae) representam um grupo de insetos com grande sucesso ecológico (Wilson, 1987). Atualmente existem 9500 espécies descritas distribuídas em aproximadamente 300 gêneros, mas estima-se que o número de espécies deva ser de 20000 em cerca de 350 gêneros (Bolton, 1995). Formigas apresentam uma ampla distribuição geográfica, sendo encontradas em altas densidades em diferentes comunidades, não ocorrendo apenas na Antártida e em algumas ilhas distantes dos continentes (Hölldobler & Wilson, 1990; Alonso & Agosti, 2000).

As formigas afetam significativamente a estrutura de diferentes ecossistemas terrestres, devido principalmente à sua abundância, diversidade de hábitos alimentares, estabilidade populacional e eficiência no forrageamento (Wilson, 1971; Hölldobler & Wilson, 1990). Outra característica marcante destes insetos é o modo de vida eusocial, que reflete um alto grau de coordenação e coesão entre indivíduos de uma colônia, com castas especializadas para determinadas tarefas e altruísmo individual (Wilson, 1971).

A composição da dieta varia grandemente entre as diferentes espécies de formigas (Carroll & Janzen, 1973; Bernstein, 1979). A maioria das espécies utiliza uma grande diversidade de artrópodes e material em decomposição (Hölldobler & Wilson, 1990). Já as espécies da tribo Attini coletam material vegetal para cultivar um fungo que é utilizado na alimentação da colônia (Hölldobler & Wilson, 1990). Muitas espécies também utilizam néctar extrafloral, secreções de insetos como homópteros e lepidópteros, bem como sementes e frutos (Oliveira & Brandão, 1991; Pizo & Oliveira, 1998; Del-Claro & Oliveira, 1999).

Além de possuírem dieta diversificada, as formigas obtêm o alimento de muitos modos diferentes. Hölldobler & Wilson (1990) classificaram as variações nas diferentes fases na obtenção de alimento como se segue. A caça pode ocorrer de maneira individual como em muitos Ponerinae (Duncan & Crewe, 1994), através de "trunk trails" até sítios com alta disponibilidade de alimento como em *Atta* e *Pogonomyrmex* (Hölldobler, 1976), ou por grupo de operárias em conjunto como nas formigas de correição (Hölldobler & Wilson, 1990). O transporte do alimento para o ninho pode ser feito por uma forrageadora solitária, através de "trunk trails", por operárias individuais recrutadas até o alimento ou por um conjunto de operárias que carrega a presa em grupo. A combinação de todos estes modos de forrageamento ocorre em diferentes espécies de formigas podendo inclusive mais de um tipo ocorrer em uma mesma espécie (Hölldobler & Wilson, 1990; Baroni-Urbani, 1993). Uma forma de aumentar a eficiência no forrageamento é o recrutamento de operárias. O recrutamento é definido como comunicação que traz outros membros da colônia para algum lugar no espaço onde trabalho é requerido (Wilson, 1971). Esta capacidade de recrutar companheiros para fontes de alimento é considerada um importante atributo para o sucesso dos insetos sociais (Wilson, 1971).

Devido a esta imensa diversidade de dieta e de estratégias utilizadas para obter o alimento, formigas são organismos muito utilizados em estudos sobre forrageamento. No entanto, para se entender como a seleção natural molda o forrageamento destes insetos é necessário um maior número de dados quantitativos sobre história natural de diferentes espécies, principalmente das pouco estudadas formigas neotropicais.

As formigas da subfamília Ponerinae têm despertado o interesse de diversos pesquisadores, principalmente pela grande diversidade comportamental e morfológica, além da presença de características consideradas ancestrais. Embora os Ponerinae sejam considerados um grupo basal entre as formigas (Wilson, 1971; Hölldobler & Wilson, 1990), esta posição vem sendo contestada em estudos cladísticos recentes (Baroni-Urbani *et al.*, 1992). A subfamília apresenta 1300 espécies descritas distribuídas em 42 gêneros e ocorre em toda região tropical (Bolton, 1995). Em geral, estas formigas apresentam características morfológicas e comportamentais ancestrais, como ninhos simples, pouco polimorfismo nas castas, e comunicação química incipiente (Wilson, 1971). Nesta subfamília existem várias estratégias de forrageamento, ocorrendo desde forrageadoras solitárias até caçadoras em grupo (Peeters & Crewe, 1987).

Dentre os Ponerinae, o gênero *Gnamptogenys* (tribo Ectatommini) é amplamente distribuído nas regiões neotropical, australiana e oriental (Lattke, 1994). Embora o gênero possua um grande número de espécies, poucas foram estudadas do ponto de vista ecológico e comportamental.

O presente trabalho investiga diversos aspectos da ecologia do forrageamento da formiga *Gnamptogenys moelleri* (Forel), uma espécie que ocorre em regiões de mata atlântica de baixada (Lattke, 1995). No primeiro capítulo são apresentados dados qualitativos e quantitativos obtidos no campo sobre a história natural e o comportamento alimentar da espécie. No segundo capítulo são apresentados experimentos em laboratório que investigam o comportamento de recrutamento da espécie frente a diferentes tipos de alimento.

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CAPÍTULO 1 - PATTERNS IN FORAGING AND NESTING ECOLOGY IN THE NEOTROPICAL PONERINE ANT *Gnamptogenys moelleri*

Abbreviated title: Ecology of the ponerine *Gnamptogenys moelleri*

Keywords: ant, foraging, *Gnamptogenys*, nesting, Ponerinae

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Resumo

Este estudo fornece dados de campo sobre a história natural e o comportamento de forrageamento da formiga Neotropical *Gnamptogenys moelleri* (Ponerinae) em uma floresta de restinga do sudeste brasileiro. Essa formiga nidifica em diferentes espécies de bromélias e seus ninhos são mais freqüentemente encontrados em bromélias grandes. *Gnamptogenys moelleri* não apresentou um padrão claro no ritmo de atividade ao longo do dia, com notável variação entre diferentes colônias. A espécie utiliza uma ampla gama de invertebrados em sua dieta, incluindo algumas presas vivas e principalmente carcaças de invertebrados. Os itens alimentares utilizados apresentaram uma grande variação em tamanho. A procura pelo alimento foi sempre realizada por operárias solitárias. Entretanto, o transporte do alimento para o ninho foi realizado por operárias solitárias (itens pequenos), ou por um grupo de operárias recrutadas que carregaram o item grande em conjunto. Praticamente toda atividade de forrageamento de *G. moelleri* foi restrita à bromélia na qual a colônia nidifica. Comparando com a estação fria e seca, na estação quente e úmida mais formigas saíram para forragear, o sucesso no forrageamento foi maior e as forrageadoras caçaram a maiores distâncias do ninho. O oportunismo na utilização de sítios de nidificação e no comportamento de forrageamento, a pequena área de caça, bem como as variações sazonais na estratégia alimentar são discutidas e comparadas com outras formigas tropicais.

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. This ant nested on different bromeliad species and the nests were more frequently found in bigger bromeliads. *Gnamptogenys moelleri* did not have a clear pattern of activity rhythm along the day, with remarkable variation among colonies. The species used a wide array of invertebrates in its diet, hunting for live prey and scavenging the majority of items from dead animals. The food items varied greatly in size. Hunting was always performed by solitary workers. Retrieving was performed by solitary workers (small items), or by a group of 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, the percentage of successful foragers was higher, and foraging trips achieved greater distances compared to the cold season. The opportunism in nest site use and foraging behaviour, the small foraging area, as well as the seasonal differences in foraging activity are discussed and compared with other tropical ants.

Introduction

Because ants employ a variety of foraging strategies and foragers usually departure from a fixed nest location, they are excellent models to test ecological and evolutionary hypotheses about foraging behaviour (Carroll & Janzen, 1973; Hölldobler & Wilson, 1990). 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 are constrained by the small amount of quantitative data on foraging behaviour in different species (Duncan & Crewe, 1994). In the Neotropics, where ant abundance and number of species are remarkable, data are still scarce. According to Tschinkel (1991), missing information on basic social insects' attributes can result in unrealistic schemes of social insect biology.

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 & Wilson, 1990). Ponerine ants may forage on the ground and on plant foliage, searching for solid and liquid food (Carroll & 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, lepidopteran larvae's secretions, as well as fruits and seeds (Carroll & Janzen, 1973; Hölldobler & Wilson, 1990; DeVries, 1991; Oliveira & Brandão, 1991; Dejean & Lachaud, 1994; Peeters, 1997; Pizo & Oliveira, 1998; Del-Claro & Oliveira, 1999). Many ponerine species are opportunistic in their choice of food items, while others are very prey-specific (Peeters & Crewe, 1987; Fresneau, 1985; Hölldobler & Wilson, 1990; Leal & Oliveira, 1995; Freitas, 1995; Fourcassié & 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 co-operative foraging mediated by varying degrees of recruitment communication between nestmates (Peeters & Crewe, 1987; Hölldobler & Wilson, 1990; Peeters, 1997). Ant foraging activity also varies with biotic factors such as the presence of parasitoids and intra and inter-specific competition, as well as abiotic factors such as temperature and humidity (Hölldobler & Wilson, 1990). Variations in these factors are likely to affect ant activity both daily and seasonally (Whitford, 1999; Orivel & Dejean, 2001; Hahn & Wheeler, 2002).

Ants in the ponerine 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 genus *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, uses chemical trails for homing, and reproduces by colony fragmentation (Gobin *et al*, 1998a and b). The presence of several gamergates or several differentiated queens in the same colony, as well as reproduction by colony fission were also reported in *Gnamptogenys striatula* (Blatrix & Jaisson, 2000; Giraud *et al.*, 2000).

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 epigaic forager in lowland forested areas (Lattke, 1995). The following aspects were studied: (1) colony demography, (2) nesting ecology, (3) daily activity rhythms, (4) diet, and (5) 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 (0-800m 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 & 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).

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 200 points were established (*ca.* 10 m apart), and the closest bromeliad to each point was tagged. 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 x 5 cm filter paper) on each bromeliad, and following loaded workers. A total of 52 bromeliads containing a *G. moelleri* colony were tagged. 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.

Activity schedule

The foraging activity of *G. moelleri* was evaluated by observing three colonies (#5, #9, #14) during the winter (June and July 2000) and three (#5, #15, #20) during the summer (February 2001). Colonies were monitored during 24 hours, in twelve 40-min sessions carried out at 2-h intervals. In each session, the number of ants leaving and returning to the nest was counted, and the air temperature and relative humidity 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 hours 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 brought to the laboratory for detailed identification (family level in most cases). The length of the items (at the longest anterior-posterior axis) was measured to the nearest 0,01mm. The items were kept in an oven at 35 °C for 24 hours, 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 hours (18:00-23:00h) 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.

Differences between summer and winter in the availability of potential arthropod prey consumed by *G. moelleri* was evaluated with sticky strip traps placed on the vegetation in July and December 2001. The trap was a 21 x 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 hours.

Statistical analyses

The frequency distribution of the bromeliads 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. 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 & Lemeshow, 1989; Hardy & Field, 1998). Spearman's coefficient was used to express the correlation between number of workers carrying a food item and the item dry weight. 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 (Figure 1). 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 ($U = 2722$; $N_1=200$; $N_2=52$; $p < 0.0001$) (Figure 2).

Activity schedule and diet

Gnamptogenys moelleri did not have a clear daily activity pattern, and presented a remarkable variation among colonies (Figure 3). Ants were active both day and night and each colony responded differently to variation in temperature and humidity (Figure 3). In general, in the winter the activity was more intense in the evening, while in the summer ants left the nest mostly during the day (Figure 3).

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 vary greatly in size (Figure 4), 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 (Figure 5A). Additionally, the number of workers carrying the item was positively correlated with item weight ($r_s = 0.643$; $n = 104$; $p < 0.0001$; Figure 5B).

Spatial foraging range in two seasons

Almost all foraging activity of *G. moelleri* is restricted to the nest bromeliad (Figure 1C and 6). During the winter, all foragers searched for food on the bromeliad leaves. In the summer some ants hunted on the ground and on nearby shrubs and trees, but the vast majority used just the bromeliad leaves (Figure 6). During the summer more ants left the nest to forage than in the winter (Figure 7A). The percent of foragers that successfully retrieved a food item was also higher in the summer (Figure 7B). The maximal distance from nest achieved by foragers in the summer was higher than in the winter (Table 4; Figure 7C). The duration of foraging trips, however, was higher in the winter than in the summer (Table 4; Figure 7D). During the winter foragers frequently remained motionless on leaves for some time (*ca.* 1 to 3 minutes), a behaviour never seen in the summer. The data from the traps revealed a marked difference between the two seasons in the overall availability of arthropods in the forest: many more arthropods were captured per trap in the summer (mean ± S.D. = 4.6 ± 3.2) than in the winter (1.8 ± 1.3; test t = 3.70; d.f. = 38; p = 0.001).

Discussion

Gnamptogenys moelleri colonies are small, with less than 200 workers in all the nests collected. This is a common characteristic of ponerine ants that contrasts with the more populous colonies found in other subfamilies such as the Formicinae, Dolichoderinae and Myrmicinae (Hölldobler & Wilson, 1990, Peeters, 1997). Most of the collected colonies had just one queen, suggesting that *G. moelleri* is a monoginous species. In contrast, immature ants were encountered in two of the queenless colonies, suggesting that gamergates (fecundated workers) may be responsible for egg laying in *G. moelleri*. The presence of gamergates has already been detected in *G. menadensis,* an Indonesian species, and *G. striatula*, an ant from Northeastern Brazil (Gobin *et al.*, 1998a, 2001; Blatrix & Jaisson, 2000; Giraud *et al.*, 2000). Additional behavioural observations are needed to confirm reproductive activity by gamergates in *G. moelleri.*

The occurrence of arboreal nests in ponerine ants, as reported in the present study, is rare. For instance, just a few species, such as *Gnamptogenys menadensis*, *Platythyrea conradti*, *Pachycondyla goeldii* and *Pachycondyla luteola* nest exclusively on vegetation (Peeters, 1997 and references therein). Among the different nests sites used by arboreal ants, bromeliads are a frequent one 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 (2) non-aquatic ones, like ant colonies, which live in the more drier parts of the plant (see Dejean & 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 plant occur in the forest (Table 2). Additionally, other ant species, such as *Odontomachus hastatus*, *Dolichoderus attelaboides*, *Camponotus* sp. and *Crematogaster* sp. may also nest in the 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 (Figure 2), and nests were more frequently found in larger bromeliads (i.e., more leaves 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 few (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 (Figure 6), larger plants represent increased foraging area and more potential prey. 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.

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 provide nutrients to plant due to accumulation of organic matter such as faeces, prey remains and dead individuals (Huxley, 1980).

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 environmental oscillations in temperature and humidity (Hölldobler & Wilson, 1990). Consequently, some species forage just during the day and others are active mostly at night. In *G. moelleri*, however, foraging activity was observed both during day and night, and colonies responded differently to variation in temperature and humidity. Continuous foraging throughout day and night has already been reported in the ponerines *Paraponera clavata* and *Odontomachus bauri* (Young & Hermann, 1980; Ehmer & Hölldobler, 1995). Therefore, other factors such as prey availability, presence of predators and parasitoids, as well as competition with other species, may be responsible for the daily foraging schedule observed in *G. moelleri* (Bernstein, 1979; Orr, 1992; Cerdá *et al.*, 1997; Del-Claro & Oliveira, 1999; Oliveira *et al.*, 1999).

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* diet is similar to that recorded for other ponerine species living in tropical forests (Fresneau, 1985; Lachaud, 1990; Dejean *et al.*, 1993; Duncan & Crewe, 1994; Pratt, 1989; Ehmer & Hölldobler, 1995; Medeiros, 1997; Pie, 1998; Fourcassié & Oliveira, 2002; Camargo, 2002). However, this pattern contrasts with other *Gnamptogenys* species exhibiting prey specialisation, such as the predominance of ants in the diet (Pratt, 1994), and specialised millipede predation (Brown, 1992). In addition to the food items recorded in this study, *G. moelleri* also collects fleshy seeds and fruits. Passos & 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 & Oliveira, 1998, 2000; Guimarães & Cogni, 2002).

Foraging strategies in the Ponerinae do not reflect phylogenetic relationship and are likely the result from unique selective pressures facing by each species (Peeters & Crewe, 1987; Hölldobler & Wilson, 1990; Peeters, 1997). The foraging strategy of *G. moelleri* has three main characteristics. First, invertebrates carcasses are generally randomly distributed in the forest, and, this may favour an individual searching strategy (Hölldobler & Wilson, 1990). Second, the vast majority of food items retrieved was scavenged from dead invertebrates. Thus, since there is no cost associated with subduing a live prey or with loosing prey due to escape, the foraging task can be performed by just one ant. Third, retrieved food items are widely variable in size (Figure 4), 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). A study of recruitment behaviour in *G. moelleri* in the laboratory is reported in chapter 2.

The foraging area of *G. moelleri* is remarkably small. Workers were observed foraging on the ground in just 6 out of 419 trips. Exclusive arboreal foraging is rare in the Ponerinae, occurring in just a few species, such as the African *Platythyrea modesta* (Djiéto-Lordon, 2001), the Neotropical *Pachycondyla goeldii* (Orivel *et al.*, 2000), and the Indonesian *Gnamptogenys menadensis* (Gobin *et al.*, 1998a). *Gnamptogenys moelleri* searches for food in a very small area, rarely leaving the nest bromeliad. The average maximal distance from nest achieved by foragers was just 0.4 m, and the ants never foraged beyond 2 m from the nest. This result contrasts with large ground-foraging ponerine species, which can go beyond 10 to 20 m from the nest to hunt (Dejean *et al.*, 1993; Dejean & Lachaud, 1994; Medeiros, 1997; Fourcassié & Oliveira, 2002). Even *Gnamptogenys menadensis*, an arboreal Indonesian species with size similar to *G. moelleri*, can reach up to 10 m from the nest (Gobin *et al.*, 1998b). This difference may result from the structure of *G. moelleri*'s nest bromeliad where many invertebrates (both live and dead) may accumulate.

Although, *G. moelleri*'s daily activity is not clearly influenced by environmental factors, its foraging activity has a marked variation between seasons. In the summer more ants leave the nest to forage, the percentage of successful trips is higher, and foragers go to greater distances than in the cold season (Figures 6, 7). Increased duration of foraging trips in the winter likely results from the fact that foragers move slower and commonly remain motionless on foliage. Seasonal variation in foraging range has already been reported in other tropical ponerine species, such as *Brachyponera senaarensis*, *Pachycondyla marginata,* and *P. striata* (Dejean & Lachaud, 1994; Leal & Oliveira, 1995; Medeiros, 1997). Seasonal oscillation in temperature and rainfall also affect ant activity indirectly through changes in the availability of food for the ants. Trap data indicated that in the summer the availability of potential arthropod prey is two times higher than in the winter. In addition, increased foraging activity in the warm months is normally associated with the presence of brood in colonies of social insects, which allocate growth to periods of high food availability (Wilson, 1971).

In conclusion, *G. moelleri* presented an opportunistic foraging behaviour, with a variable daily foraging schedule, and 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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Tables

Table 1. Composition of five colonies of *Gnamptogenys moelleri* collected in the cold 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 queen	No. of eggs	No. of larvae	No. of pupae	No. of female alates	No. of male alates	No. of 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

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)
Quesnelia arvensis	G	83	60
Vriesea phillippocoburgii	E	10	12
Vriesea sp. 1	E	6	12
Aechemea nudicaulis	E	2	6
Nidularium sp.	G	0	2
Vriesea sp. 2	E	0	1
Undetermined 1	G, E	0	6
Undetermined 2	G	0	2

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
MIRIAPODA		
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		
Crysomelidae	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)	

Table 4. Effects of season (cold *x* warm) and colony observed on the maximal distance achieved by foraging workers, and duration of foraging trip of *Gnamptogenys moelleri* in the sandy plain forest of Ilha do Cardoso, Southeast Brazil. Data were log transformed for the two-factor analysis of variance.

	Maximal distance				Duration of trip			
	d.f	M.S.	F	P	d.f	M.S.	F	P
Season	1	0.79	21.04	**<0.001**	1	2.08	19.10	**<0.001**
Colony	2	0.04	1.16	NS	2	0.29	2.69	NS
Season X colony	2	0.03	0.762	NS	2	0.10	0.91	NS
Error	415	0.04			415	0.11		

Figure 5. *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.

Figure 6. Spatial distribution of foraging activity of three colonies of *Gnamptogenys moelleri* in the cold season and in the warm period, in the sandy plain forest of Ilha do Cardoso, Southeast Brazil. Values represent the number of ants observed in each location during continuous 5-hour observation sessions in each season.

Figure 7. Seasonal foraging activity of *Gnamptogenys moelleri* in the sandy plain forest of Ilha do Cardoso, Southeast Brazil. Three colonies were continuously observed during 5 hour sessions in each season. (A) Number of foragers leaving the nest. (B) Percentage of foragers returning with food. (C) Maximal distance from nest achieved by foraging workers. (D) Duration of foraging trips. On (A) and (B) each dot represents a colony. On (C) and (D) 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 and the open circles represent far outside values.

Figure 5. *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.

Figure 6. Spatial distribution of foraging activity of three colonies of *Gnamptogenys moelleri* in the cold season and in the warm period, in the sandy plain forest of Ilha do Cardoso, Southeast Brazil. Values represent the number of ants observed in each location during continuous 5-hour observation sessions in each season.

Figure 7. Seasonal foraging activity of *Gnamptogenys moelleri* in the sandy plain forest of Ilha do Cardoso, Southeast Brazil. Three colonies were continuously observed during 5 hour sessions in each season. (A) Number of foragers leaving the nest. (B) Percentage of foragers returning with food. (C) Maximal distance from nest achieved by foraging workers. (D) Duration of foraging trips. On (A) and (B) each dot represents a colony. On (C) and (D) 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 and the open circles represent far outside values.

Figures

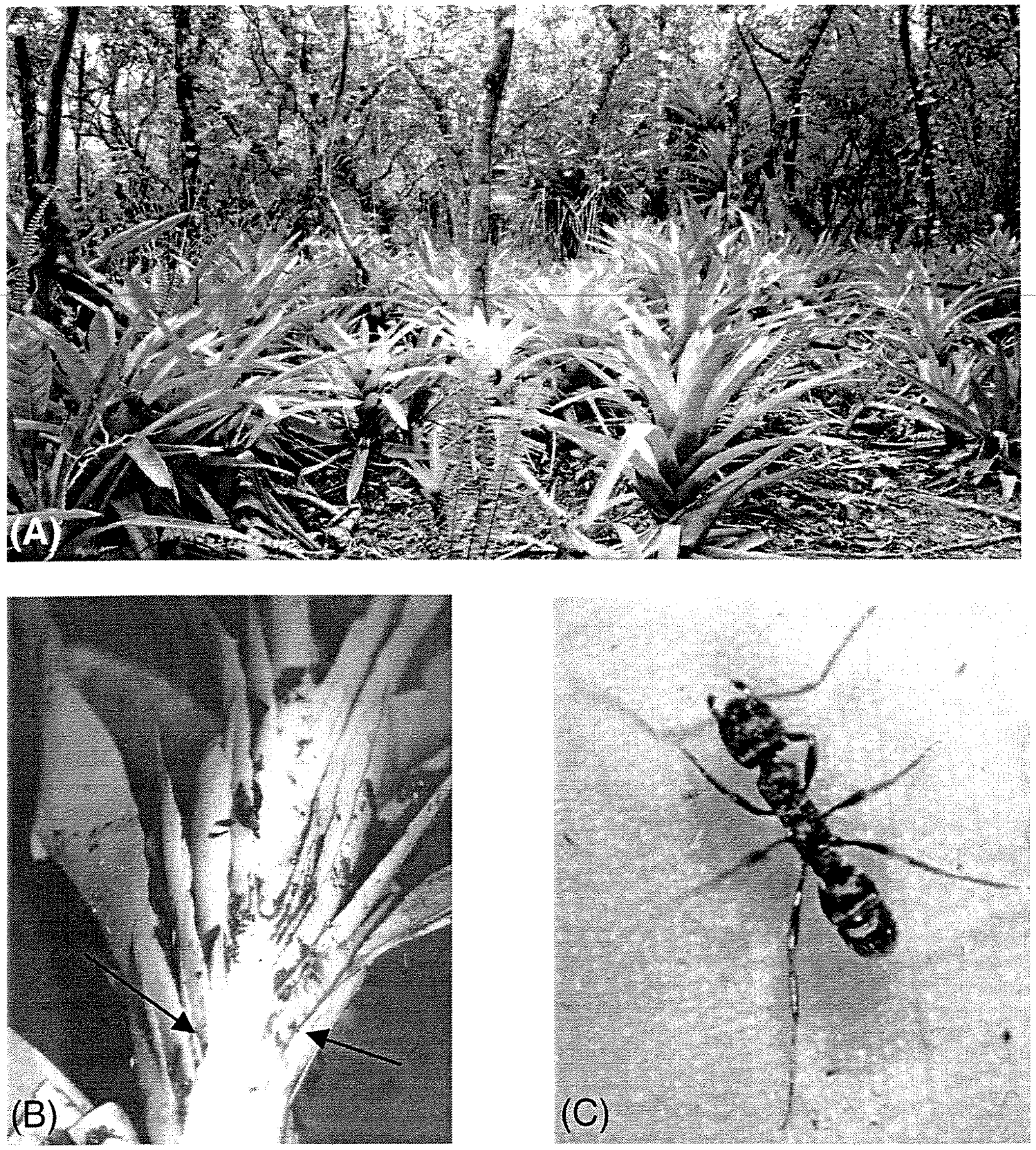

Figure 1

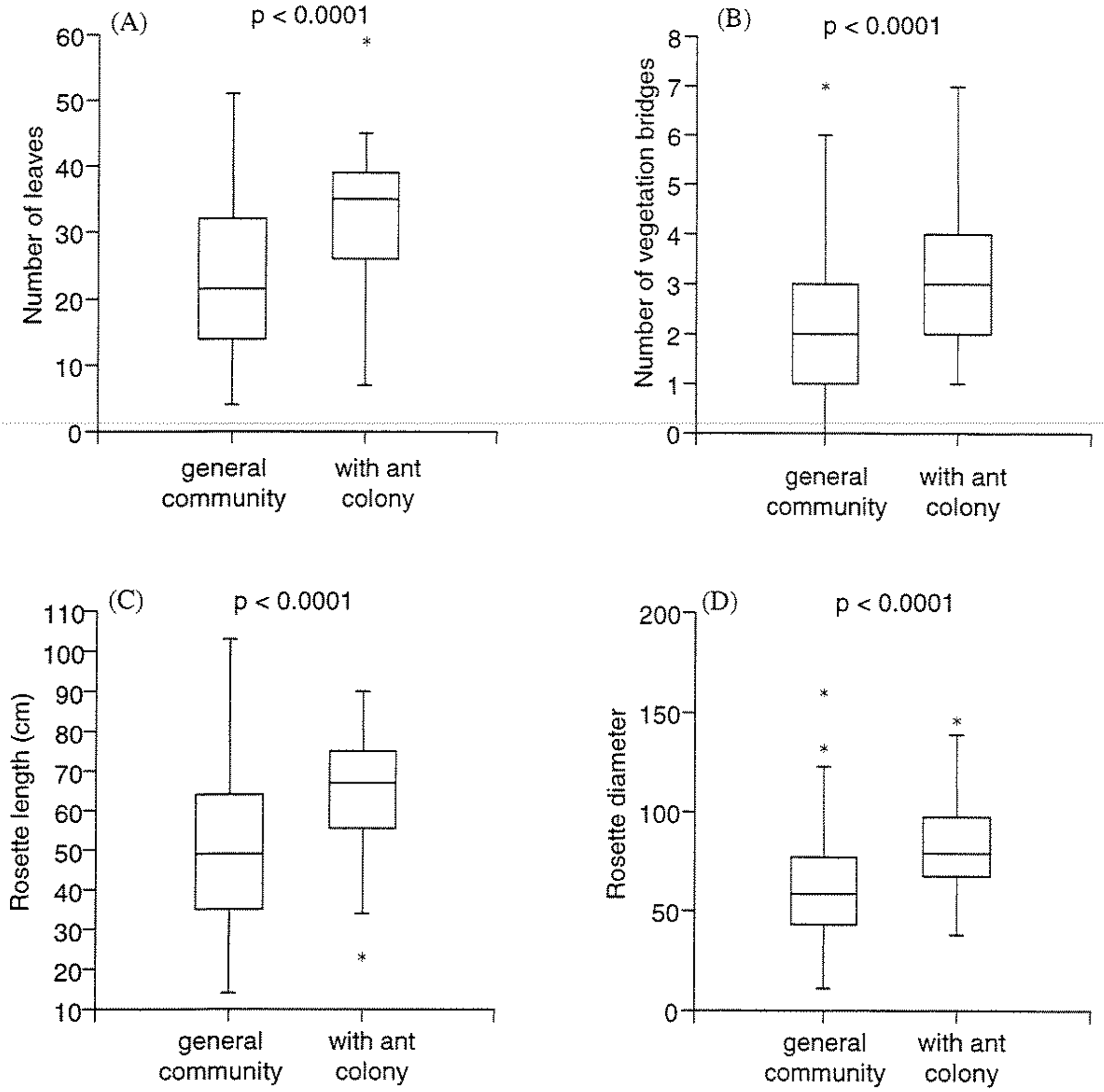
(A)
p < 0.0001
Number of leaves
0
10
20
30
40
50
60
general community
with ant colony
(B)
p < 0.0001
Number of vegetation bridges
0
1
2
3
4
5
6
7
8
general community
with ant colony
(C)
p < 0.0001
Rosette length (cm)
10
20
30
40
50
60
70
80
90
100
110
general community
with ant colony
(D)
p < 0.0001
Rosette diameter
0
50
100
150
200
general community
with ant colony

Figure 2

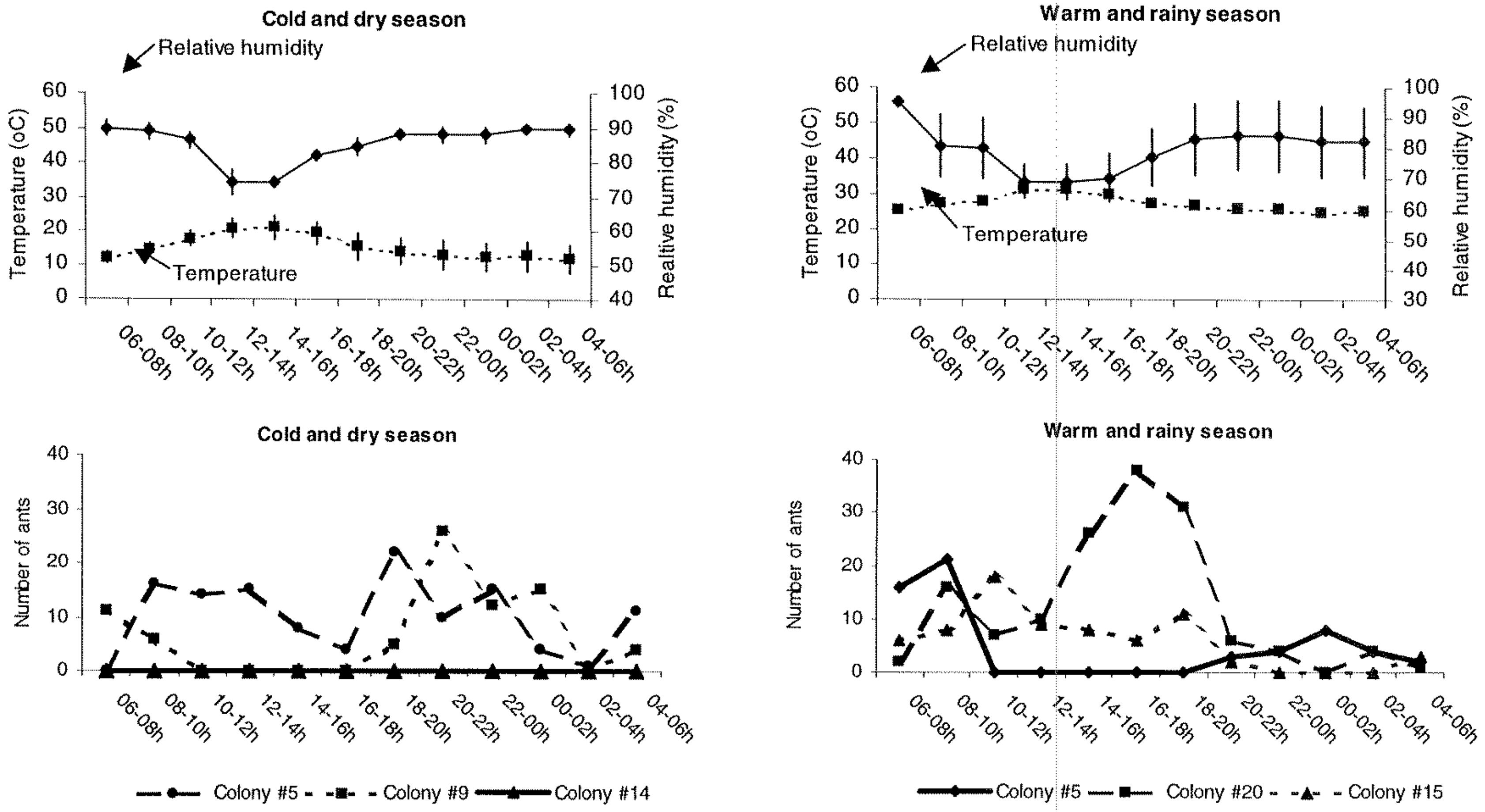
Cold and dry season
Relative humidity
Temperature
Temperature (oC)
60
50
40
30
20
10
0
Realtive humidity (%)
100
90
80
70
60
50
40
06-08h
08-10h
10-12h
12-14h
14-16h
16-18h
18-20h
20-22h
22-00h
00-02h
02-04h
04-06h
Warm and rainy season
Relative humidity
Temperature
Temperature (oC)
Relative humidity (%)
30
Cold and dry season
Number of ants
Colony #5
Colony #9
Colony #14
Warm and rainy season
Number of ants
Colony #5
Colony #20
Colony #15

Figure 3

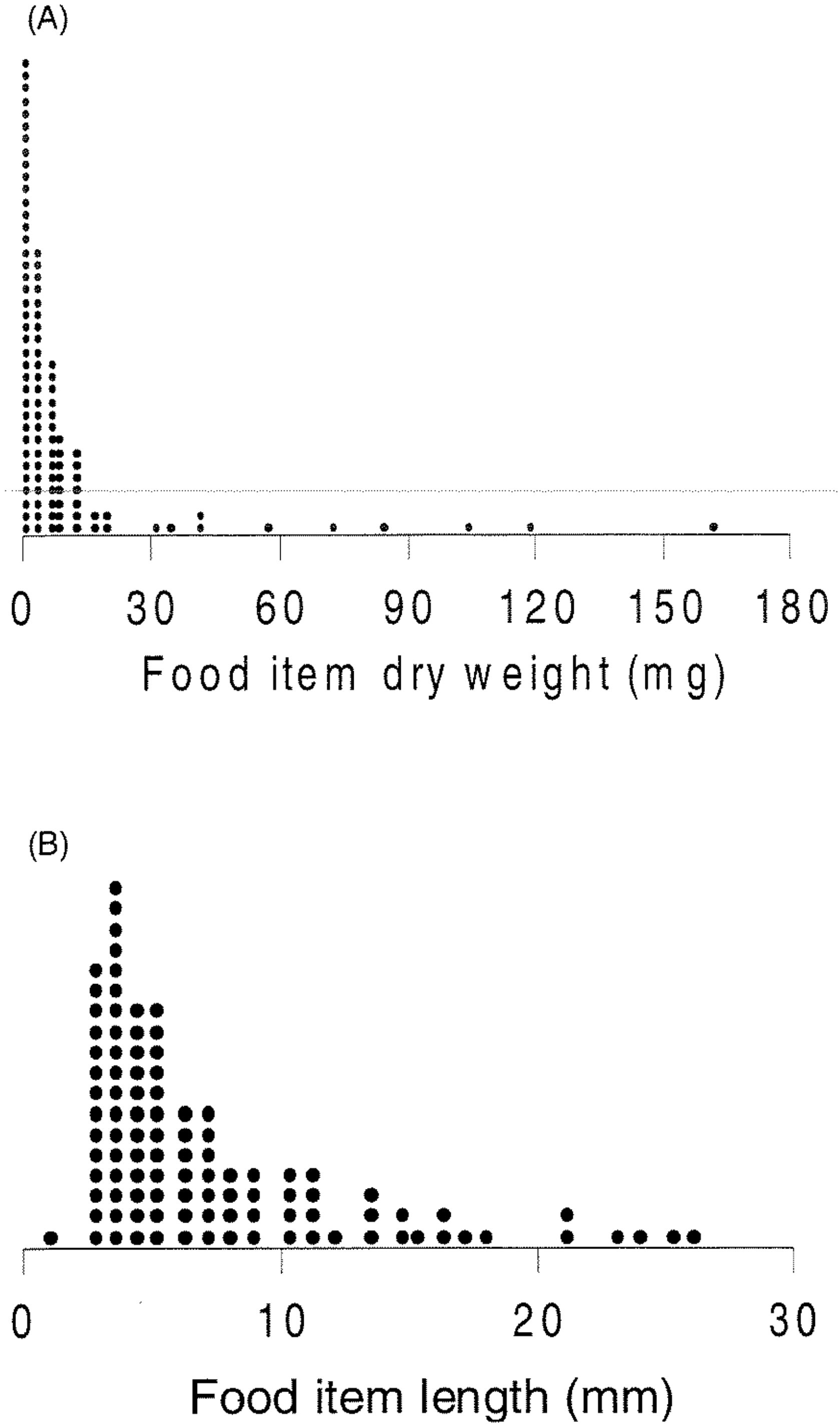
(A)
0
30
60
90
120
150
180
Food item dry weight (mg)
(B)
0
10
20
30
Food item length (mm)

Figure 4

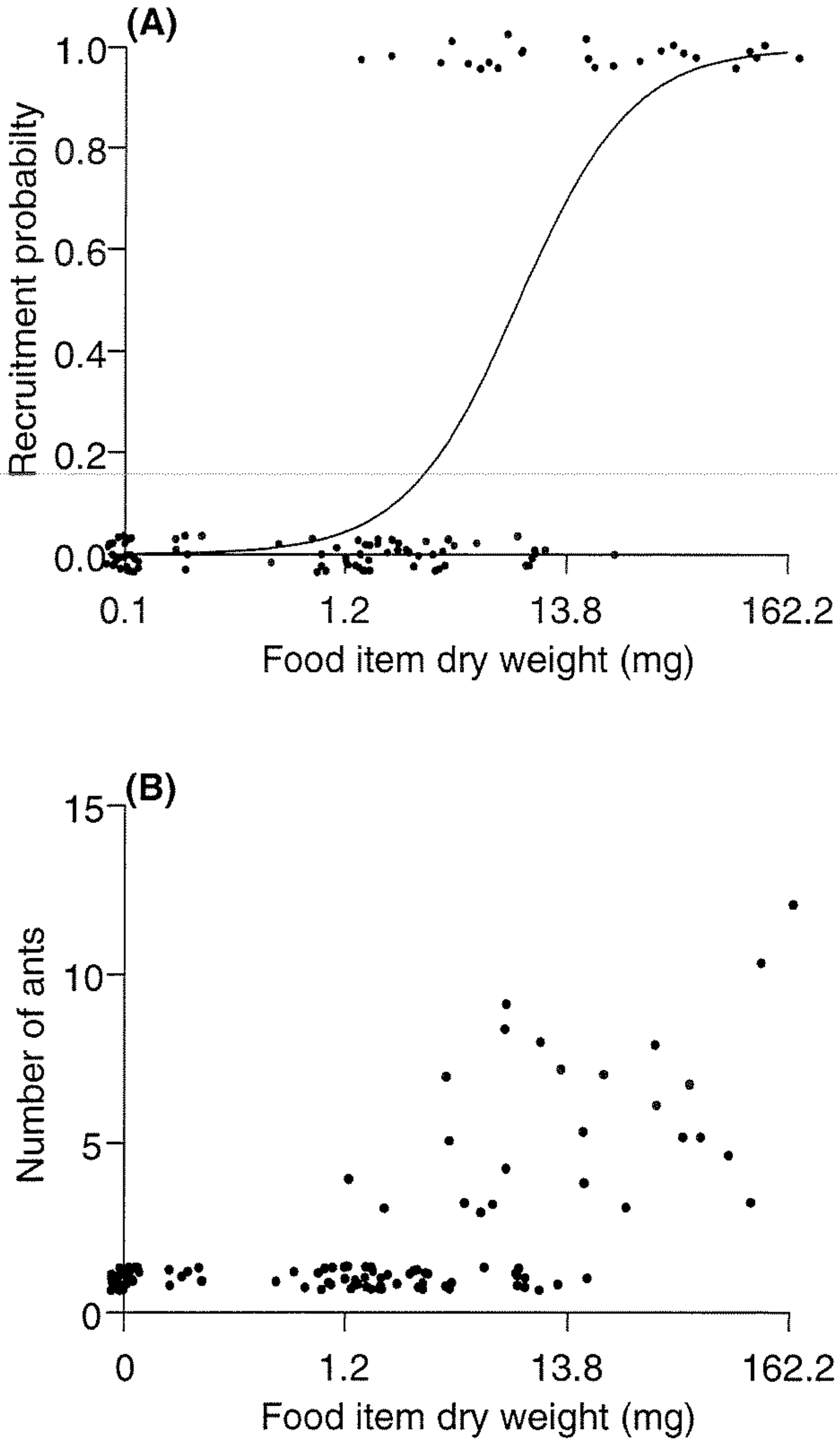
(A)
1.0
0.8
0.6
0.4
0.2
0.0
Recruitment probabilty
0.1
1.2
13.8
162.2
Food item dry weight (mg)
(B)
15
10
5
0
Number of ants
0
1.2
13.8
162.2
Food item dry weight (mg)

Figure 5

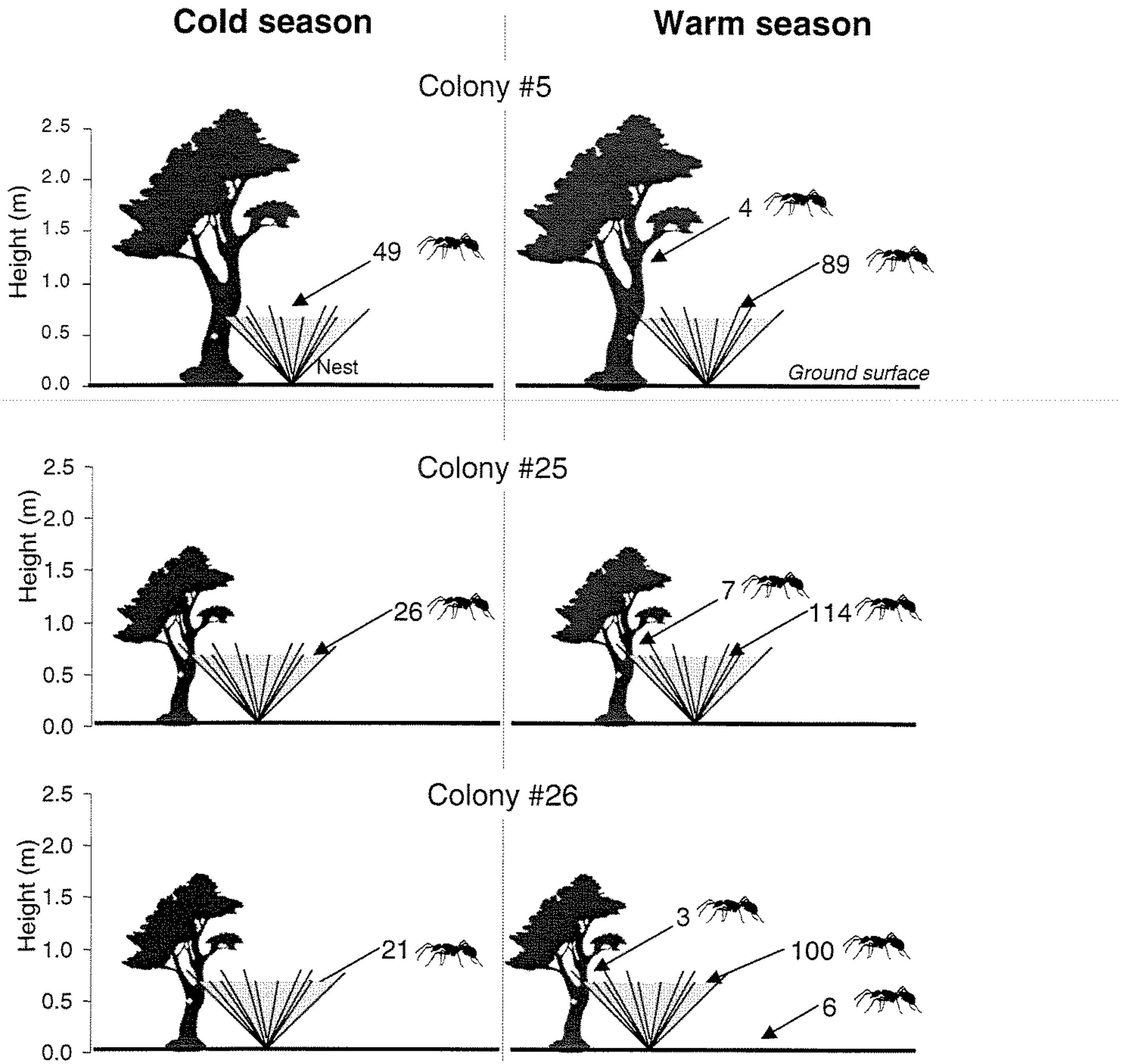
Cold season
Warm season
Colony #5
2.5
2.0
1.5
1.0
0.5
0.0
Height (m)
49
Nest
4
89
Ground surface
Colony #25
26
7
114
Colony #26
21
3
100
6

Figure 6

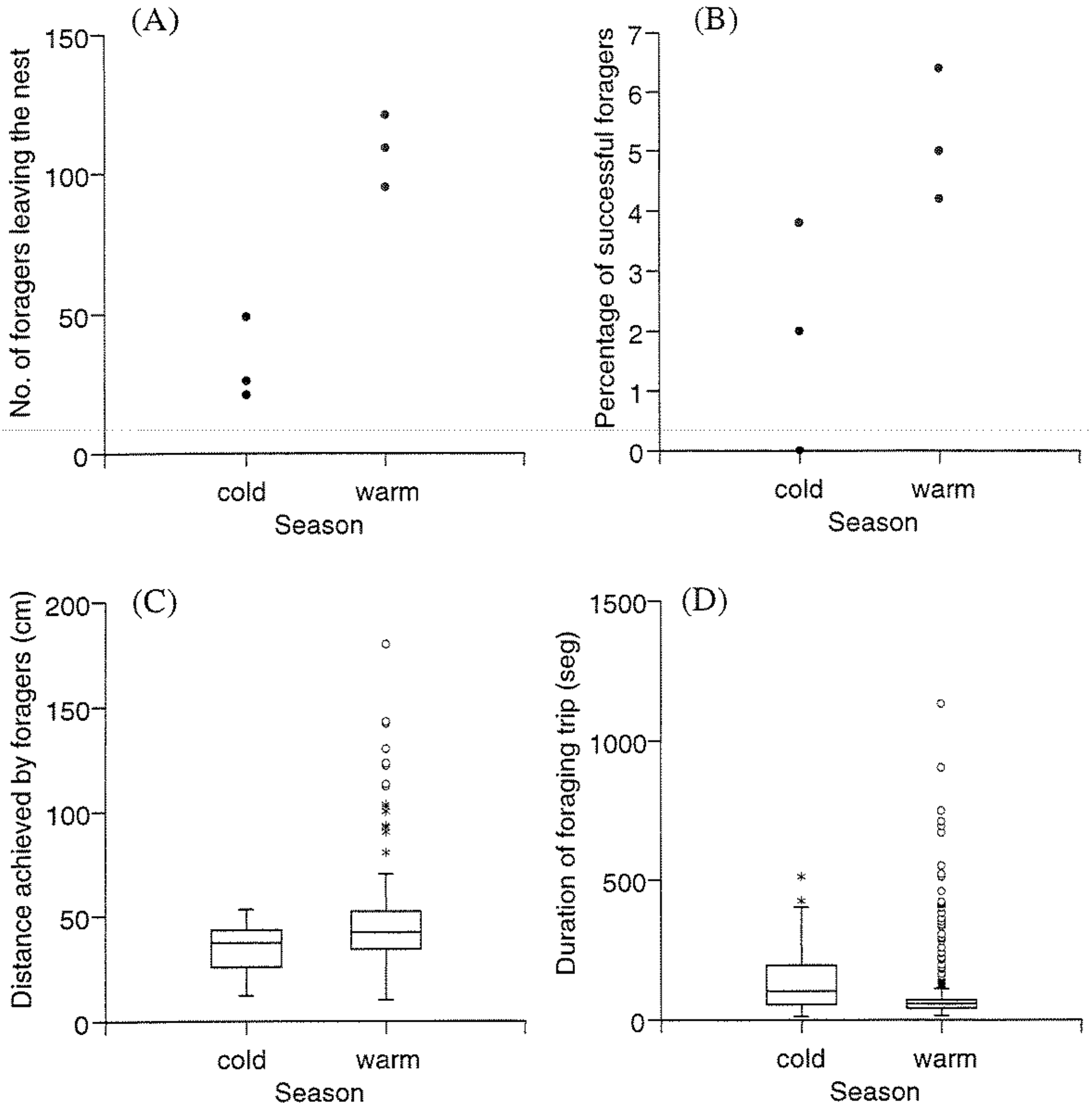
(A)
No. of foragers leaving the nest
150
100
50
0
cold
warm
Season
(B)
Percentage of successful foragers
7
6
5
4
3
2
1
0
cold
warm
Season
(C)
Distance achieved by foragers (cm)
200
150
100
50
0
cold
warm
Season
(D)
Duration of foraging trip (seg)
1500
1000
500
0
cold
warm
Season

Figure 7

CAPÍTULO 2- RECRUITMENT BEHAVIOUR DURING FORAGING IN THE NEOTROPICAL ANT *Gnamptogenys moelleri* (FORMICIDAE: PONERINAE): DOES THE TYPE OF FOOD MATTER?

Running title: Recruitment behaviour in *Gnamptogenys*

Keywords: ant behaviour, communication, Ectatommini, solitary foraging, group retrieval

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Resumo

Este estudo investiga o comportamento de recrutamento da formiga neotropical *Gnamptogenys moelleri* (Ponerinae) em laboratório. Três tipos de alimento foram utilizados nos experimentos: solução de açúcar, inseto grande e um agregado de insetos pequenos. Com todos os três tipos de alimento, o primeiro encontro por uma forrageadora resultou em uma maior número de formigas saindo do ninho e encontrando o alimento na arena. Experimentos adicionais mostraram que quando uma operária de *G. moelleri* encontra solução de açúcar ou um inseto grande, esta retorna para o ninho e transmite informação sobre a localização do alimento, através da marcação do substrato. As formigas recrutadas carregam o inseto grande em grupo para o ninho. No entanto, quando uma operária encontra um agregado de insetos pequenos, não ocorre transmissão de informação sobre a localização do alimento e o retorno de uma forrageadora que obteve sucesso induz outras operárias a saírem do ninho e forragear, mas para nenhum local em particular. A natureza da informação sobre a localização do alimento, bem como as possíveis vantagens no campo da flexibilidade na estratégia de forrageamento são discutidas.

Summary

This study investigates the recruitment behaviour of the neotropical ponerine ant *Gnamptogenys moelleri* in laboratory. Three types of food were used in the experiments: liquid food, large insect, and group of small insects. For all the three types of food, the first encounter by a *G. moelleri* forager resulted in a higher number of ants leaving the nest and finding the food in the arena. Further experiments showed that, after finding liquid food or large prey, the *G. moelleri* forager returns to the nest and transmits information to nestmates about food location on the substrate. Recruited ants collectively retrieved the large insect to the nest. On the other hand, when a forager encounters a cluster of small prey, there is no transmission of information to nestmates about food location, although the return of successful foragers induces nestmates to leave nest and hunt. The nature of the information about food location transmitted to nestmates, as well as the possible advantages in the field of this flexible foraging strategy are discussed.

Introduction

Foraging mode may vary widely among ants, ranging from solitary hunting without any co-operation during search and food retrieval, to different levels of co-operative foraging mediated by different types of recruitment communication between nestmates (Carrol & Janzen, 1973; Traniello, 1989; Hölldobler & Wilson, 1990). The ability to recruit nestmates to profitable food sources is considered an important attribute leading to the ecological and evolutionary success of social insects (Wilson, 1971). Recruitment behaviour during foraging activity occurs when a scout ant returns to the nest after having discovered a food source, and transmits information concerning food location to inactive foragers in the nest. There are three basic types of recruitment behaviour during foraging in ants: (1) *tandem running*, in which the scout guides just one recruit to the food item; (2) *group recruitment*, in which the scout guides a group of ants to the food; and (3) *mass recruitment*, in which a trail laid by the recruiter while returning to the nest guides recruits to the food and these recruits can become recruiters in their turn (see Attygalle & Morgan, 1985; Beckers *et al.*, 1989; Hölldobler & Wilson, 1990; Liefke *et al.*, 2001). Foraging strategies among ants do not reflect phylogenetic relationships and probably result from unique selective pressures on each species (Hölldobler, 1984a; Baroni-Urbani, 1993). For instance, in the subfamily Ponerinae recruitment trail communication has evolved independently many times and five different trail-pheromone glands have already been identified (Hölldobler & Wilson, 1990).

Ants in the genus *Gnamptogenys* (Ponerinae) 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*, belonging to the tribe Ectatommini, a derived *taxa* in the Ponerinae

(Lattke, 1994; Keller, 2000). Most *Gnamptogenys* species are considered rare and cryptic, and very few had their behaviour and ecology studied (Pratt, 1994; Gobin *et al.*, 1998a and b, and 2001; Blatrix & Jaisson, 2000; Giraud *et al.*, 2000; Blatrix *et al.*, 2002). Pratt (1994) has presented evidence that *G. horni* recruits nestmates to food sources in the laboratory. *Gnamptogenys menadensis* uses chemical trails during homing (Gobin *et al.*, 1998b). In addition, esters from the Dufour's gland have been identified as a trail pheromone in the South American species *G. striatula*, but the ecological circumstances in which the trail is used have not been determined (Blatrix *et al.*, 2002).

Gnamptogenys moelleri is a medium-size (*ca.* 0.5 cm) ant that occurs in Neotropical lowland forested areas (Lattke, 1995). The species nests in bromeliads, and forages almost exclusively on the nest plant (Chapter 1). *Gnamptogenys moelleri* uses a wide array of invertebrates in its diet, hunting for live prey and, most frequently, scavenging for dead animals. Hunting is always performed by solitary workers, while retrieving is performed both by solitary workers for small food items, or by a group of recruited workers (3-12 ants) who collectively transports large food items. The probability of a worker to recruit nestmates increased with the size of the food item in the field, and the number of workers carrying the item was positively correlated with its weight (Chapter 1).

This study investigates the recruitment behaviour of *G. moelleri* when fed with different types of food. Five questions were addressed: (1) Is there an increase in the number of ants leaving the nest after a worker had encountered food? (2) Is there an increase in the number of ants encountering the food, after a worker had first encountered it? (3) Does the first worker encountering food transmit information about food location to nestmates? (4) Is the information about food location transmitted on the substrate? (5) Do these behavioural responses vary with the type of food? To answer these questions a set of controlled experiments were carried out in the laboratory.

Captive colonies, and general experimental procedures

Six *Gnamptogenys moelleri* colonies were collected at 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 (Barros *et al.*, 1991). All colonies were nesting in bromeliads, were queenright, had plenty of brood (eggs, larvae and pupae), and had 50 to 186 workers. The colonies were cultured at 23 – 26°C and diffusely illuminated from above during day hours. Each colony was housed in one glass tube (2.2 cm diameter x 15 cm length) containing water trapped at the end behind a cotton plug. The glass tube was placed in a nest box (40 x 20 cm) connected to a foraging arena (40 x 20 cm) by a small bridge. The ants were fed three times a week with freshly killed *Drosophila* flies, *Tenebrium* larvae, cockroaches, diluted honey, and synthetic ant diet (Bhatkar & Whitcomb, 1970). Colonies were starved for 24 hours prior to the experiments. All experiments were carried out between 7:00 and 16:00 h, and were replicated in each of the six cultured colonies. Control and treatment manipulations were randomly assigned to each colony in all experiments. Control and experimental manipulations were separated by at least 4 days in each colony.

Three types of food were used in the experiments: (A) liquid food -- 2 ml of honey solution (50%) on a plastic dish (3.5 cm diameter); (B) a large (*ca.* 3 cm) freshly killed cockroach, and (C) a group 20 freshly killed adult *Drosophila* flies (1mm).

Experiment 1

Methods

This experiment aimed to determine if the encounter of food by a forager causes an increase in the number of ants that leave the nest and find the food in the arena (50 cm from the nest entrance). After the discovery of food by a foraging ant, the number of ants leaving the nest, and the number of ants finding the food were counted during 2 min intervals along 10 min. Ant performance was tested with the three types of food described above. Control tests relative to each type of food consisted of placing in the arena: (A) a plastic dish without honey solution; (B) a piece of polystyrene (3 cm), and (C) 20 pieces of polystyrene (1mm each).

Results

Both the number of ants leaving the nest and encountering the food, after the first forager had discovered food in the arena greatly surpassed the respective controls, irrespective of the type of food (Figures 1, 2).

Upon discovering the honey solution or the cockroach, the first forager inspected the food with the antenna and apparently tasted it. After this, the successful scout returned to the nest tapping the sting onto the substrate (Figure 3). With the cockroach, however, before returning to the nest the forager tried unsuccessfully to retrieve the large prey by vigorously biting and pulling its legs. When the returning ant entered the nest, nestmates exhibited increased locomotory activity. The successful scout then quickly left the nest and returned to the food, again tapping the sting onto the substrate. Subsequently, nestmates left the nest tapping the antenna on the substrate, and reached the food source. A few ants, however, returned to the nest without finding the food. In the cockroach experiment, the large prey was invariably carried to the nest by a group of ants (Figure 4). Ants behaved differently towards *Drosophila* prey. The first forager to find the flies stung one of them and carried it to the nest. However, the returning ant did not tap the sting onto the substrate. When the successful scout entered the nest some of the ants began to leave the nest and eventually found the flies. The original scout that had encountered the *Drosophila* returned repeatedly to the food source and retrieved several flies in succession.

Experiment 2

Methods

To test whether the first forager to find food transmits information about food location to nestmates, the following experiment was carried out with each of the three types of food. Two cardboard bridges (40 x 3 cm) connected the nest box to each of two separate locations (A and B) in the foraging arena, as shown in Figure 5. In the control observations the food was placed in location A, while in location B no food was provided. After the first ant had discovered food, the number of ants walking over each bridge was recorded for 5 min. In the experimental manipulations, food was placed in location A, and location B remained rewardless. After the first ant had encountered the food, however, the reward was transferred to location B. The number of ants walking over each bridge was then recorded from 0 to 5 min, and from 15 to 20 min. The number of ants walking over each bridge was compared with a paired t-test.

Results

In control tests, more ants walked over the bridge leading to the honey solution dish than over the bridge leading to the location deprived of food ($t = 6.3$, d.f. = 5, $p = 0.001$; Figure 6A). After the relocation of food following its discovery by a scout ant, more ants walked over the bridge leading to the previous food location (A) in the first 5 min than over the bridge leading to the current location (B) of the honey solution ($t = 11.0$, d.f. = 5, $p < 0.001$; Figure 6B). However, 15 min after food relocation ant traffic was higher over the bridge leading to the current food location (B) than over the bridge where honey solution was first encountered (location A) ($t = 7.9$, d.f. = 5, $p = 0.001$; Figure 6C). The same behavioural pattern was observed in the experiment using a cockroach as food source (control: $t = 6.5$, d.f. = 5, $p = 0.001$; food relocation 0-5 min: $t = 7.4$, d.f. = 5, $p = 0.001$; food relocation 15-20 min: $t = 7.7$, d.f. = 5, $p = 0.001$) (Figure 7A-C).

Results from the experiment using *Drosophila* flies as food source differed markedly from the above pattern. Ant traffic over the bridges was similar after the flies had been discovered by a forager at location A ($t = 2.0$, d.f. = 5, $p = 0.10$; Figure 8A). The pattern did not change after 5 min ($t = 1.5$, d.f. = 5, $p = 0.20$) or 15 min ($t = 0.4$, d.f. = 5, $p = 0.69$) since the location of food source had been shifted (Figure 8B,C).

Experiment 3

Methods

The aim of this experiment was to determine if the information about food location is transmitted on the substrate. The same experimental set with the two bridges described above was used. The only food types used were honey solution and cockroach, since experiment 2 showed that there is no information about food location when the food source is the *Drosophila* cluster. The food was placed in location A, and after the first forager had encountered it and returned to the nest, the food was removed from the arena and the bridges were swapped. The number of ants reaching location A or B over 5 min was recorded and compared with paired t-tests.

Results

After the bridges had been swapped, the number of ants reaching location B (no food) was higher than the number of ants reaching location A (where food had been discovered prior the experimental manipulation). Results were significant using either a honey solution (t = 5.8; d.f. = 5; p = 0.002) or a cockroach (t = 3.4; d.f. = 5; p = 0.02) as the food source (Figure 9A, B).

Experiment 4

Methods

Since ants foraging on the honey often dampened their legs on the solution, the following experiment was carried out to test if the remains of honey on the substrate could provide information about food location to the ants. The same experimental set with two bridges was used. The honey solution was placed in location A, while location B received no food. After the first scout ant had encountered food and returned to the nest, the honey solution and the two bridges were removed. In control test, the bridges were replaced by two fresh ones. In the experimental manipulation the used bridges were each replaced by a fresh bridge leading to location A, and by a new bridge artificially damped with honey solution leading to location B. This bridge was daubed with a brush bristle damped in honey solution, simulating the ants footsteps on the substrate. The number of ants reaching location A or B over 5 min was recorded and compared with paired t-tests.

Results

The number of ants reaching each location was similar in the control situation (t = 0.35; d.f. = 5; p = 0.74; Figure 10A) as well as after the experimental manipulation (t = 0.34; d.f. = 5; p = 0.74; Figure 10B).

Discussion

The discovery of food by a *G. moelleri* forager resulted invariably in higher numbers of ants leaving the nest and finding the food source in the arena, irrespective of the type of food. Recruitment behaviour in *G. moelleri*, however, does not necessarily contain information about food location. Further experimentation showed that when a forager encounters an aggregation of small prey, there is no transmission of information to nestmates about food location. In this case retrieval of food to the nest stimulates other ants to leave and, as a result, the number of ants finding the clustered prey also increases. This behaviour, called social facilitation (Wilson, 1971), in which the return of successful foragers induces others to go out and hunt, but to no particular location, is common in ponerine species such as *Ophthalmopone berthoudi*, *Odontomachus bauri* and *Ectatomma permagnum* (Peeters & Crewe, 1987; Oliveira & Hölldobler, 1989; Paiva & Brandão, 1989). In some species, group retrieving of a food item can occur even without recruitment. This happens when a scout ant attracts nestmates in her immediate vicinity through the release of an alarm pheromone, a behaviour clearly not equivalent to returning to the nest to recruit nestmates (Peeters & Crewe, 1987). Nevertheless, when a *G. moelleri* forager finds liquid food or a large prey, it returns to the nest and transmits recruitment signals to nestmates that leave the nest. Additional directional information about food location is transmitted onto the substrate by the recruiting ant. In the case of the liquid food, our tests showed that remains of honey solution on the substrate provide no directional clue to ants about food location. Therefore the foraging strategy employed by *G. moelleri* is flexible, and depends on the kind of food encountered. Flexibility in foraging behaviour related to food type and size has already been reported in *Paraponera* and *Ectatomma* species (Overal, 1986; Breed *et al.*, 1987; Schatz *et al.*, 1997). This flexibility permits colony adjustments to environmental changes in an adaptive way, and allows the utilisation of alternate food sources by specialist species (Lachaud & Dejean, 1994), or the exploration of a wider range of food items by generalist species such as *G. moelleri* (Hölldobler, 1984b; Dejean *et al.*, 1993).

Gnamptogenys moelleri has a limited spatial foraging range, which is restricted mostly to the leaves of the nest bromeliad (Chapter 1). Since the small size of *G. moelleri* workers (*ca.* 0.5 cm) precludes single foragers from retrieving large prey, recruitment of nestmates widens the size range of food items available to the colony (Chapter 1; Traniello, 1987). Additionally, by recruiting nestmates the colony may avoid losing the food to competitors (Hölldobler & Wilson, 1990; Cerdá *et al.*, 1997), which can occur in case of both large prey and liquid food (see Breed *et al.*, 1987).

If *G. moelleri* is able to recruit and direct nestmates towards food sources, why this is not observed in case of small clustered prey? Field observations revealed that only 24% of food items are retrieved in group by *G. moelleri* colonies, and this occurred for items larger than 7 mm (Chapter 1). Solitary *G. moelleri* foragers are able to retrieve small clustered insects by making successive trips, as also reported for *Ectatomma quadridens*

(Overal, 1986). However, retrieving aggregate prey individually in several trips may take longer than retrieving in cooperation with recruited nestmates. This extra time could allow competitors to exploit the source, and ultimately result in the loss of the food. Sequential individual retrieving may occur in *G. moelleri* because foragers may be unable to detect surplus prey in the immediate vicinity. In the laboratory, when approaching the aggregated *Drosophila*, the scout ant invariably stung and retrieved the first fly it seized, returning immediately to the nest, possibly without noticing the surplus prey nearby. Clusters of small prey may not be common in the field; in fact the vast majority of the food items retrieved by *G. moelleri* was scavenged from dead invertebrates that in general are randomly distributed in the forest (Chapter 1).

Directional recruitment information in *G. moelleri* is transmitted on the substrate probably by a trail pheromone produced by the Dufour's gland, as previously documented for the ponerines *Ectatomma ruidum*, *Gnamptogenys menadensis* and *G. striatula* (Pratt, 1989; Bestmann *et al.*, 1995; Gobin *et al.*, 1998b; Blatrix *et al.*, 2002), which are phylogenetically very close to *G. moelleri* (Lattke, 1994; Keller, 2000). Even though the gland secreting the trail pheromone has never been investigated in *G. moelleri*, the tapping of the sting onto the substrate is very similar to the behaviour described in *Ectatomma ruidum* (Figure 3; Pratt, 1989). The use of Dufour's gland is rare among ponerine ants, since most species in this subfamily use secretion from poison or pygidial gland for trail communication (Hölldobler & Wilson, 1990). Even though different recruitment behaviours in ants are thought to have been convergently selected in different species by similar population/environment constraints (Baroni-Urbani, 1993), Dufour's gland in the Ectatommini may indicate a phylogenetic trend in glandular use. Field studies have shown that *G. moelleri* has a generalised diet that includes both live and dead invertebrates, as well as sugar solution, and the food items consumed vary greatly in size. The present study shows that a flexible foraging strategy allows *G. moelleri* colonies to consume a diversity of food items in the field. Recruitment behaviour and glandular sources of trail pheromones in other Ectatommini species, and the ecological contexts in which trails are laid are promising topics that warrant future investigations.

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Figure Legends

Figure 1. Number of *Gnamptogenys moelleri* workers leaving the nest after an ant had discovered: (A) a dish with honey solution (white bar), or an empty dish (grey bar); (B) a 3 cm freshly killed cockroach (white bar), or a 3 cm piece of polystyrene (grey bar); (C) a cluster of 20 freshly killed *Drosophila* flies (white bar), or a cluster of 20 small pieces of polystyrene (grey bar). Values are means + 1 SE (n=6 colonies).

Figure 2. Number of *Gnamptogenys moelleri* workers encountering food or control objects after an ant had discovered: (A) a dish with honey solution (white bar), or an empty dish (grey bar); (B) a 3cm freshly killed cockroach (white bar), or a 3cm piece of polystyrene (grey bar); (C) a cluster of 20 freshly killed *Drosophila* flies (white bar) or a cluster of 20 small pieces of polystyrene (grey bar). Values are mean + 1 SE (n=6 colonies).

Figure 3. (A) A *Gnamptogenys moelleri* forager walking in its normal position. (B) A forager tapping the sting onto the substrate when returning to the nest after finding a big insect or honey solution.

Figure 4. Several *Gnamptogenys moelleri* workers carrying a large cockroach to their nest, in the laboratory.

Figure 5. Diagram of the artificial settings used on the *G. moelleri* recruitment communication experiments 2, 3 and 4. The cardboard bridges depart from the same place, but lead to two different locations.

Figure 6. (A) Number of *Gnamptogenys moelleri* workers gathering at a honey solution after the first ant had encountered the food at location A. (B), (C) After the first ant had encountered the honey solution at location A, the food was shifted to location B. After food relocation the number of ants gathering at the two locations was counted over (B) initial 5 min, and (C) from 15 to 20 min. Values are means + 1 SE (n=6 colonies).

Figure 7. (A) Number of *Gnamptogenys moelleri* workers gathering at a freshly killed cockroach after the first ant had encountered the food at location A. (B), (C) After the first ant had encountered the freshly killed cockroach at location A, the food was shifted to location B. After food relocation the number of ants gathering at the two locations was counted (B) over initial 5 min, and (C) from 15 to 20 min. Values are means + 1 SE (n=6 colonies).

Figure 8. (A) Number of *Gnamptogenys moelleri* workers gathering at a cluster of 20 freshly killed *Drosophila* flies after the first ant had encountered the food at location A. (B), (C) After the first ant had encountered the cluster of 20 freshly killed *Drosophila* flies at location A, the food was shifted to location B. After food relocation the number of ants gathering at the two locations was counted (B) over initial 5 min, and (C) from 15 to 20 min. Values are means + 1 SE (n=6 colonies).

Figure 9. Number of *Gnamptogenys moelleri* workers gathering at a food source location. After the first ant had encountered food and returned to the nest, the two bridges were

swapped, and food was removed. Data in (A) (honey solution) and (B) (cockroach) shows ant traffic to either location over 5 min. Values are means + 1 SE (n=6 colonies).

Figure 10. Number of *Gnamptogenys moelleri* workers gathering at honey solution at location A. After the first ant had encountered food and returned to the nest, the honey solution was removed, and the two bridges were each (A) replaced by two new fresh bridges, (B) replaced by a fresh bridge and a new bridge artificially daubed with honey solution. Data shows intensity of ant traffic over the bridges during 5 min after experimental manipulation. Values are means + 1 SE (n=6 colonies).

Figures

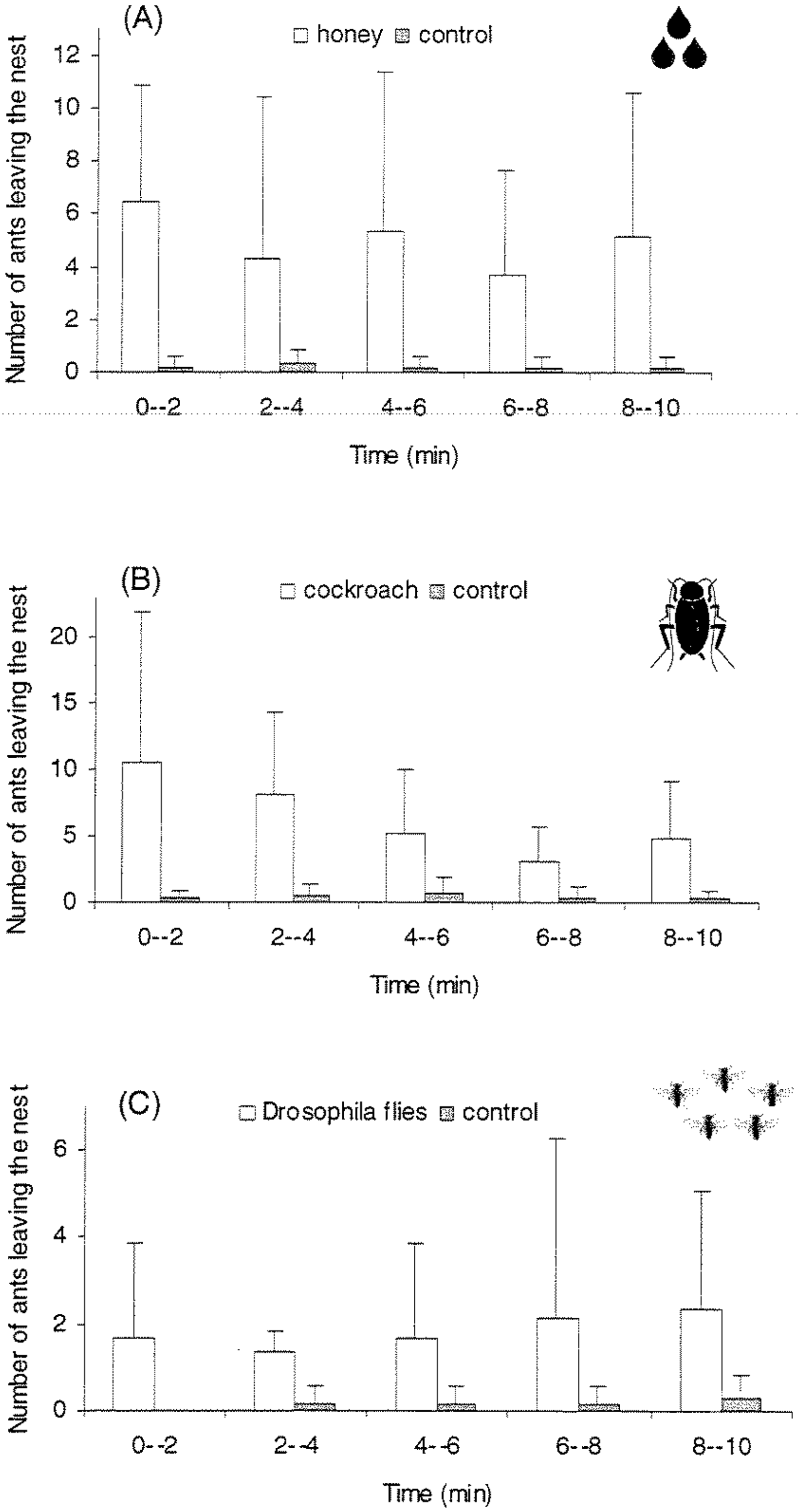

Figure 1

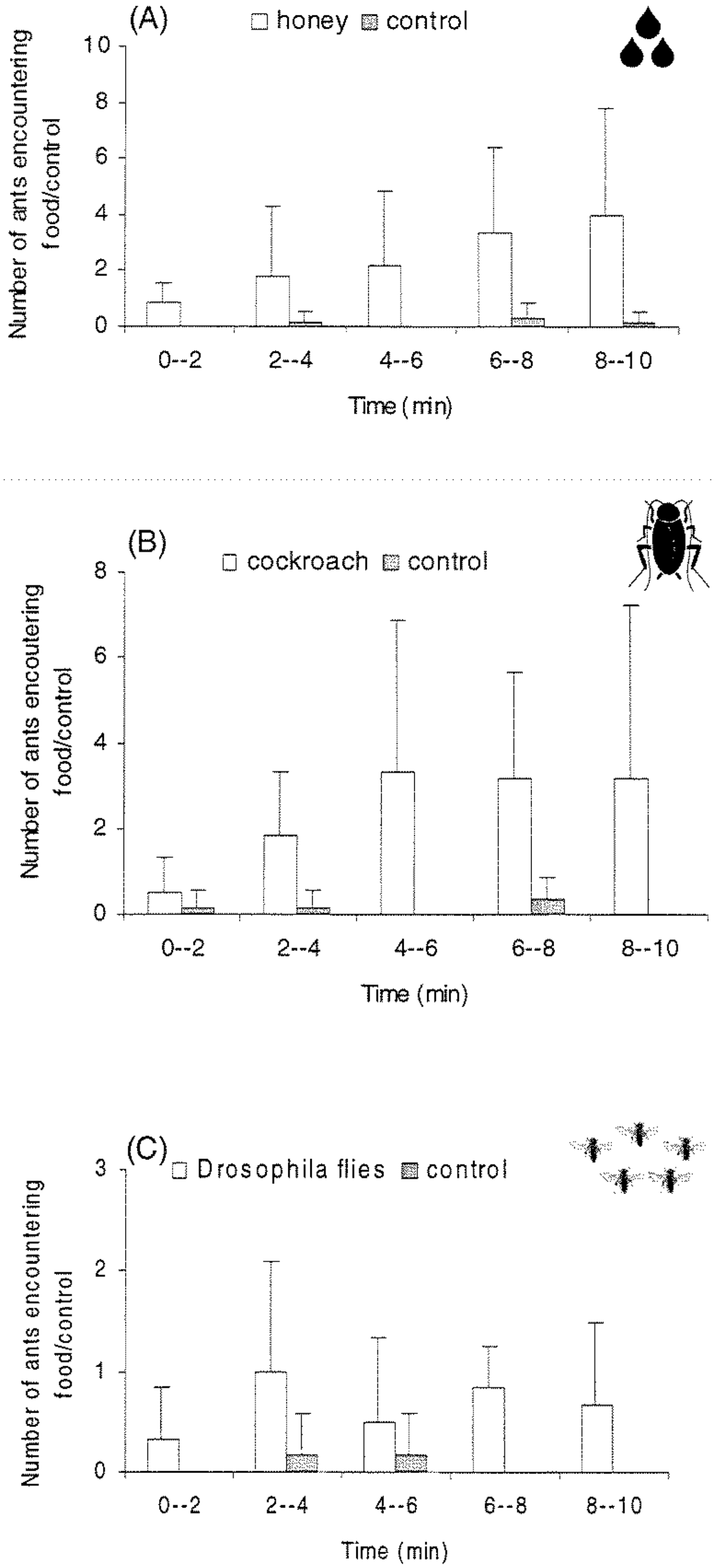
(A)
□ honey ▨ control
Number of ants encountering food/control
0
2
4
6
8
10
0--2
2--4
4--6
6--8
8--10
Time (min)
(B)
□ cockroach ▨ control
Number of ants encoutering food/control
0
2
4
6
8
0--2
2--4
4--6
6--8
8--10
Time (min)
(C)
□ Drosophila flies ▨ control
Number of ants encountering food/control
0
1
2
3
0--2
2--4
4--6
6--8
8--10
Time (min)

Figure 2

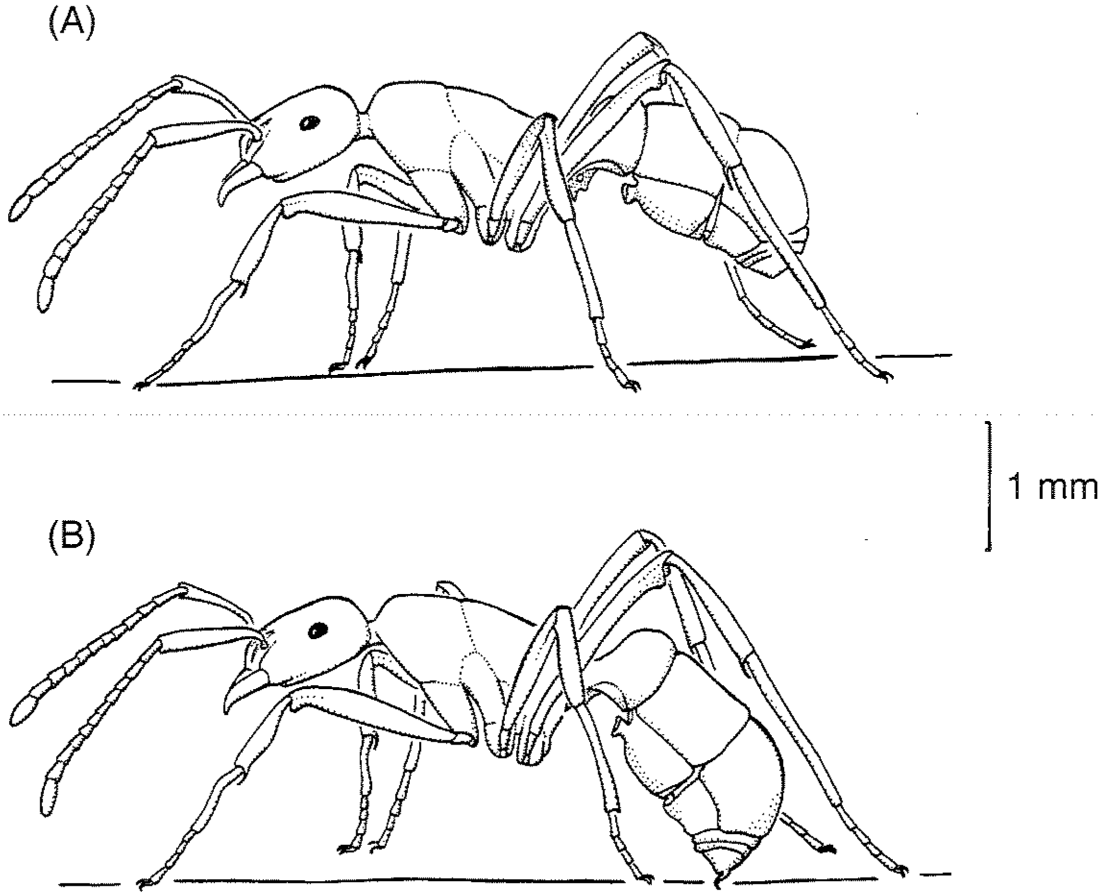

Figure 3

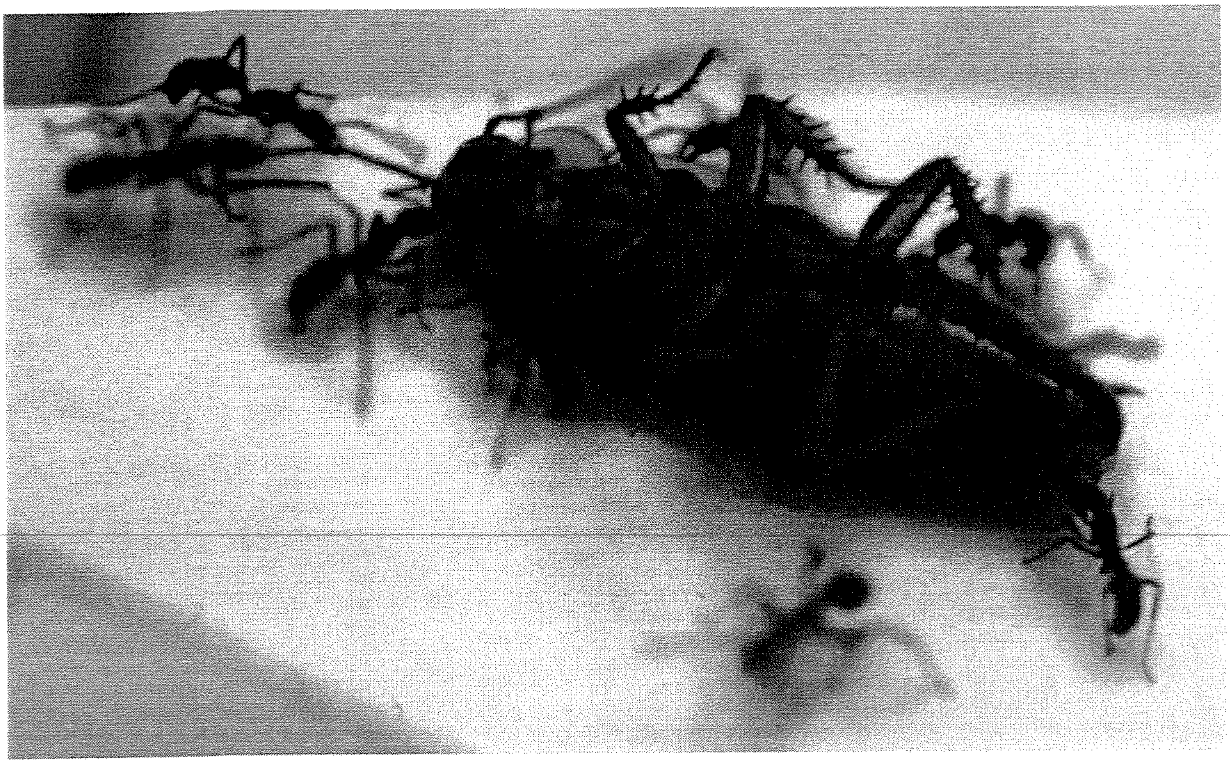

Figure 4

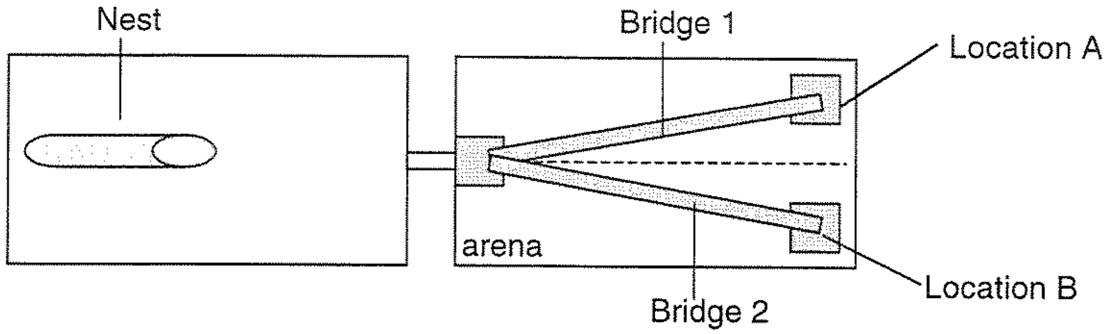

Figure 5

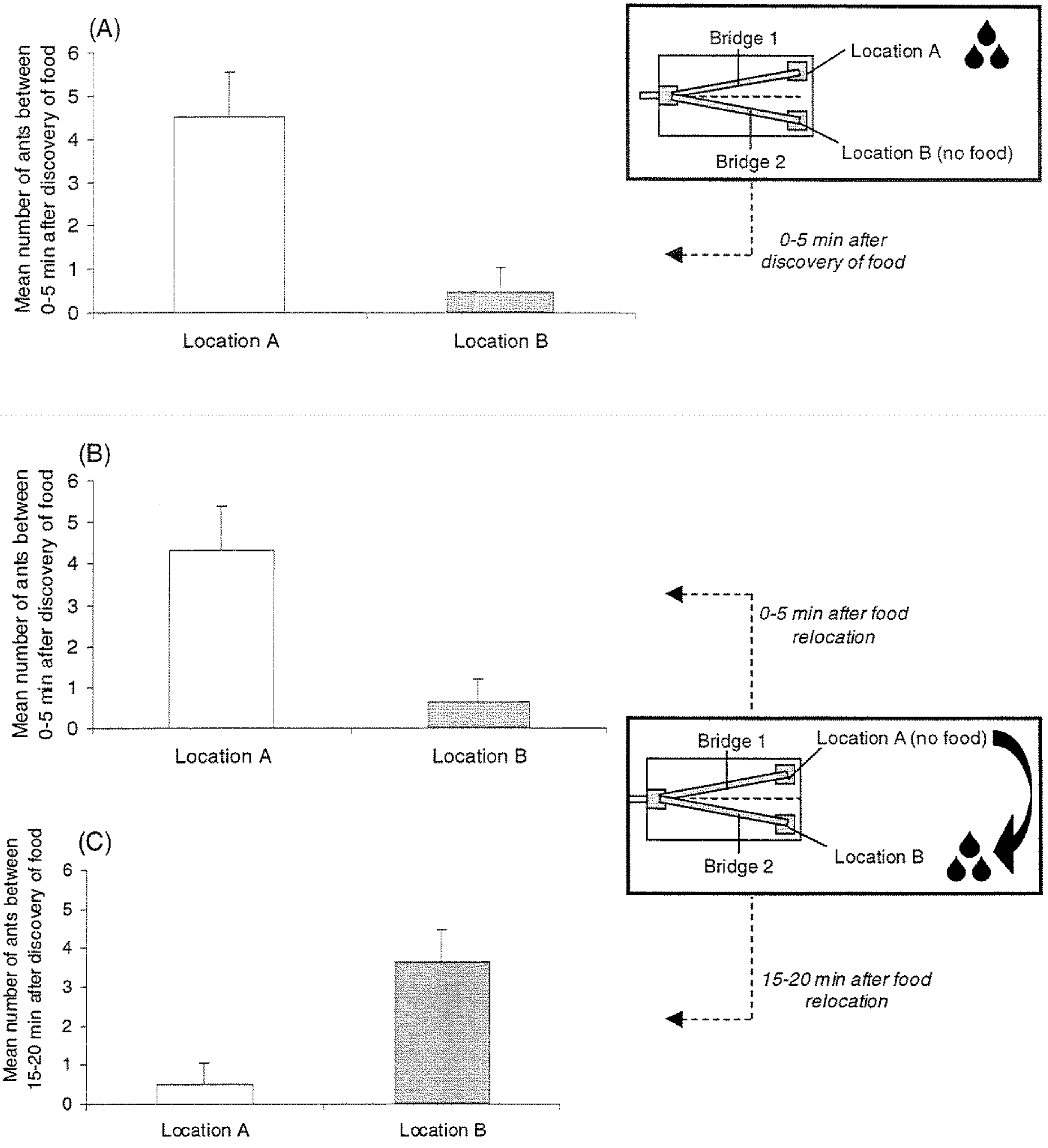
(A)
Mean number of ants between 0-5 min after discovery of food
0
1
2
3
4
5
6
Location A
Location B
Bridge 1
Location A
Bridge 2
Location B (no food)
0-5 min after discovery of food
(B)
Mean number of ants between 0-5 min after discovery of food
0
1
2
3
4
5
6
Location A
Location B
0-5 min after food relocation
Bridge 1
Location A (no food)
Bridge 2
Location B
15-20 min after food relocation
(C)
Mean number of ants between 15-20 min after discovery of food
0
1
2
3
4
5
6
Location A
Location B

Figure 6

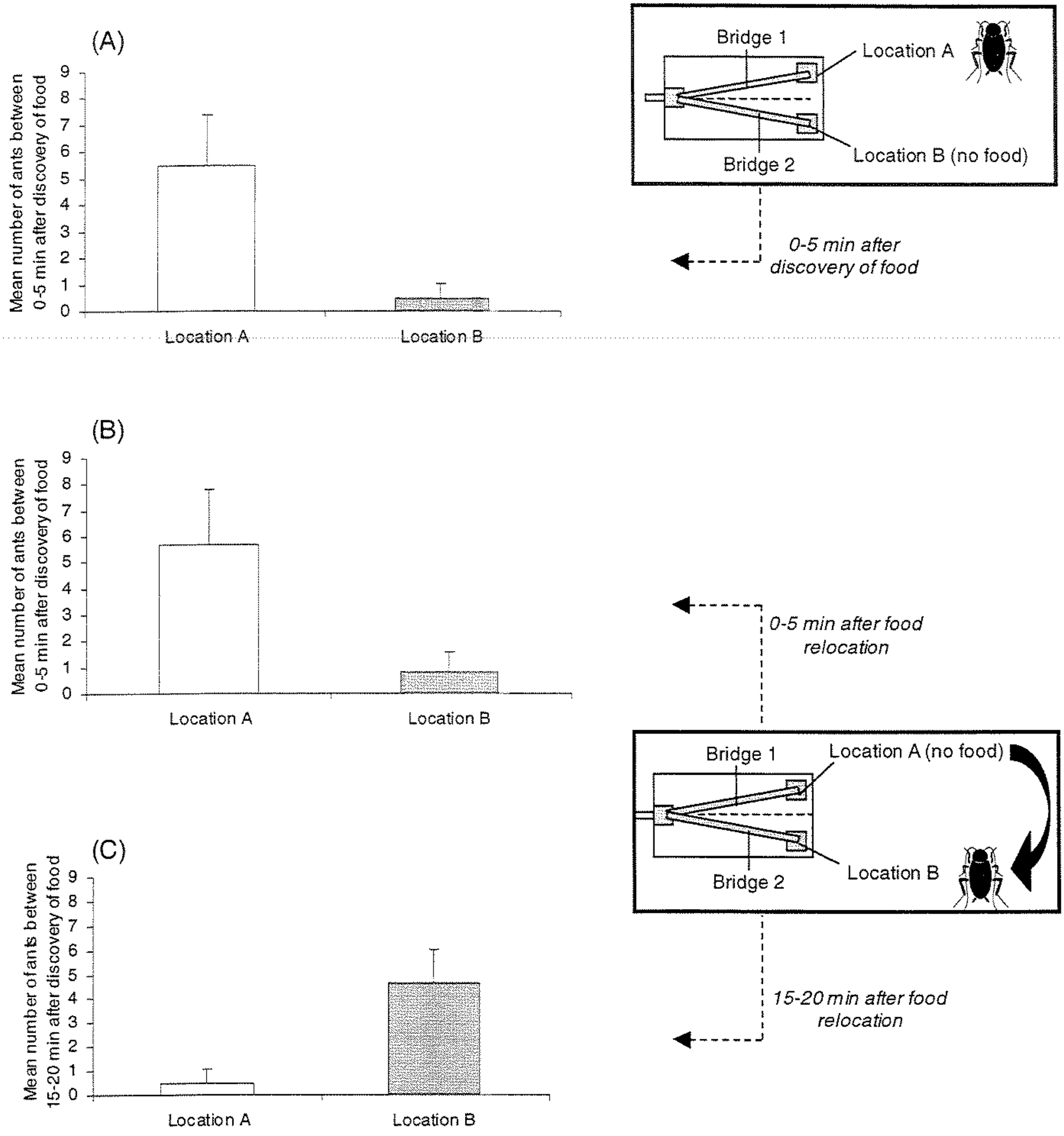
(A)
Mean number of ants between 0-5 min after discovery of food
0
1
2
3
4
5
6
7
8
9
Location A
Location B
Bridge 1
Location A
Bridge 2
Location B (no food)
0-5 min after discovery of food
(B)
Mean number of ants between 0-5 min after discovery of food
0
1
2
3
4
5
6
7
8
9
Location A
Location B
0-5 min after food relocation
Bridge 1
Location A (no food)
Bridge 2
Location B
15-20 min after food relocation
(C)
Mean number of ants between 15-20 min after discovery of food
0
1
2
3
4
5
6
7
8
9
Location A
Location B

Figure 7

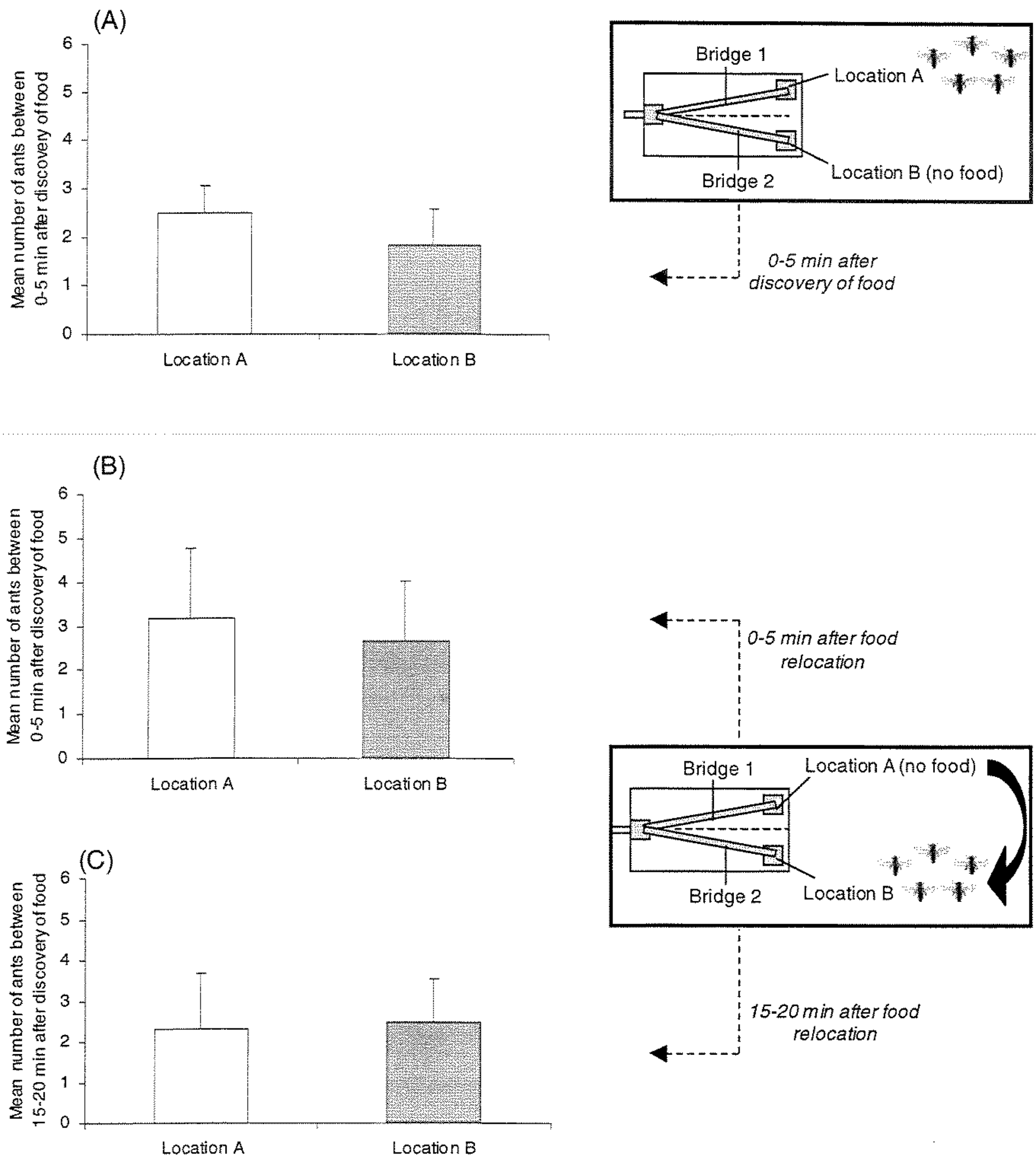
(A)
Mean number of ants between 0-5 min after discovery of food
0
1
2
3
4
5
6
Location A
Location B
Bridge 1
Location A
Bridge 2
Location B (no food)
0-5 min after discovery of food
(B)
Mean number of ants between 0-5 min after discovery of food
0
1
2
3
4
5
6
Location A
Location B
0-5 min after food relocation
Bridge 1
Location A (no food)
Bridge 2
Location B
(C)
Mean number of ants between 15-20 min after discovery of food
0
1
2
3
4
5
6
Location A
Location B
15-20 min after food relocation

Figure 8

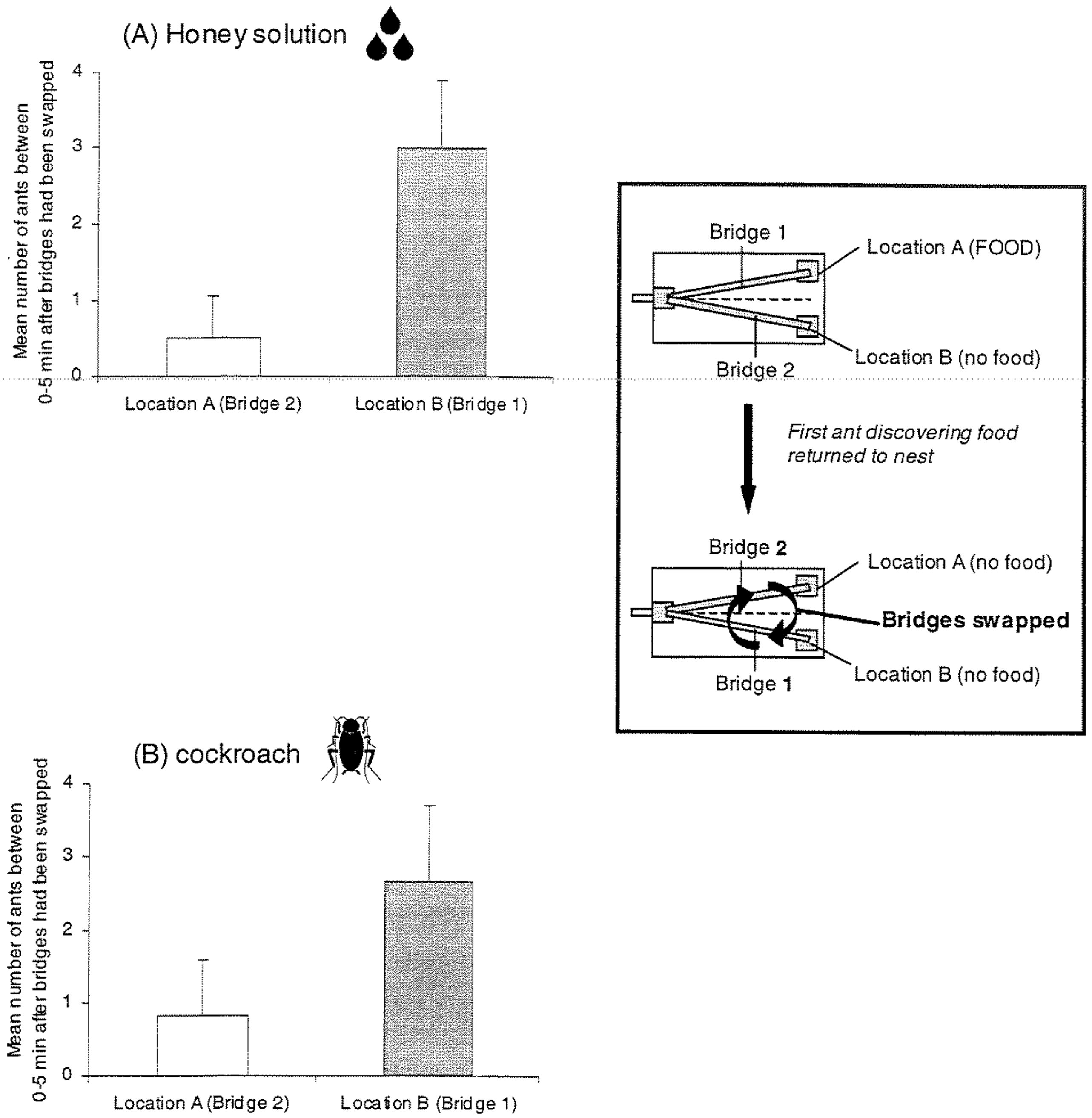
(A) Honey solution
Mean number of ants between 0-5 min after bridges had been swapped
4
3
2
1
0
Location A (Bridge 2)
Location B (Bridge 1)
Bridge 1
Location A (FOOD)
Location B (no food)
Bridge 2
First ant discovering food returned to nest
Bridge 2
Location A (no food)
Bridges swapped
Location B (no food)
Bridge 1
(B) cockroach
Mean number of ants between 0-5 min after bridges had been swapped
4
3
2
1
0
Location A (Bridge 2)
Location B (Bridge 1)

Figure 9

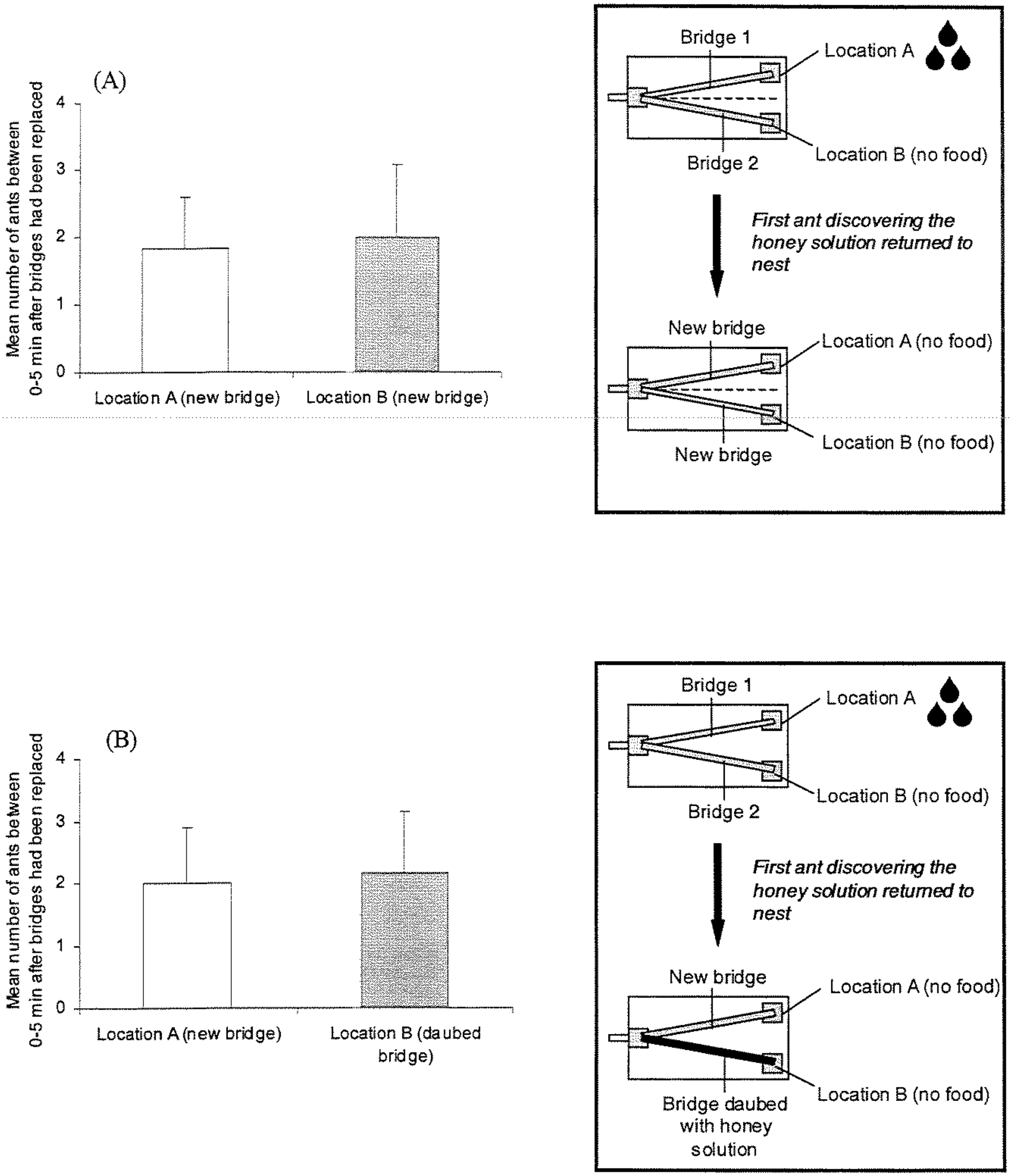
(A)
Mean number of ants between 0-5 min after bridges had been replaced
0
1
2
3
4
Location A (new bridge)
Location B (new bridge)
Bridge 1
Location A
Bridge 2
Location B (no food)
First ant discovering the honey solution returned to nest
New bridge
Location A (no food)
New bridge
Location B (no food)
(B)
Mean number of ants between 0-5 min after bridges had been replaced
0
1
2
3
4
Location A (new bridge)
Location B (daubed bridge)
Bridge 1
Location A
Bridge 2
Location B (no food)
First ant discovering the honey solution returned to nest
New bridge
Location A (no food)
Bridge daubed with honey solution
Location B (no food)

Figure 10

CONCLUSÃO GERAL

Gnamptogenys moelleri apresenta um comportamento alimentar oportunista, com um ritmo diário de atividade variável, e uso flexível de itens alimentares que incluem invertebrados (vivos e mortos) e néctar. Além disso, o comportamento de recrutamento permite à colônia o carregamento de itens alimentares grandes, aumentando o espectro de tamanho dos itens alimentares utilizados. A atividade de forrageamento apresentou uma grande variação sazonal que provavelmente resulta das oscilações de fatores físicos, bem como das oscilações na disponibilidade de alimento. *Gnamptogenys moelleri* também se mostrou oportunista ao utilizar diferentes espécies de bromélias como ninho. Ninhos foram mais freqüentemente encontrados em bromélias grandes, e este padrão está provavelmente relacionado à extensão espacial de forrageamento da espécie, que é restrita à bromélia na qual a colônia nidifica.

Gnamptogenys moelleri utiliza diferentes estratégias ao forragear. Quando uma operária encontra um item alimentar pequeno, esta retorna para o ninho carregando-o sozinha. O retorno para o ninho de uma operária com alimento sempre provoca a saída de um maior número de operárias para forragear, independentemente do tipo de alimento. Quando uma operária encontra solução açucarada ou um item alimentar grande, esta retorna para o ninho e outras operárias começam a sair do ninho para forragear. A transmissão de informação sobre o local do item alimentar ocorre através da marcação química sobre o substrato. Deste modo, itens grandes são carregados para o ninho por um grupo de operárias recrutadas. Esta flexibilidade na estratégia de forrageamento, bem como a capacidade de recrutar operárias, parecem ter evoluído como uma forma de aumentar o intervalo de tamanhos de presas disponíveis na restrita área de forrageamento da colônia.

O sucesso no desenvolvimento de modelos e hipóteses sobre estratégias de forrageamento depende da disponibilidade de dados quantitativos sobre o comportamento de forrageamento de diferentes espécies. Além disso, dados quantitativos sobre a história natural, ecologia e comportamento de uma espécie animal, como os apresentados neste estudo, permitem a ligação entre fatores ecológicos e estratégias de forrageamento, bem como o estabelecimento de novas hipóteses sobre os processos responsáveis pelos padrões observados.