Seasonal Patterns in Activity Rhythm and Foraging Ecology in the Neotropical Forest-Dwelling Ant, *Odontomachus chelifer* (Formicidae: Ponerinae)

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ABSTRACT   We provide qualitative and quantitative data on the natural history and foraging behavior of the ground-dwelling ant *Odontomachus chelifer* (Latreille) (Formicidae: Ponerinae) in a forest reserve in southeastern Brazil, with emphasis on colony activity rhythms and diet preferences in relation to seasonal availability of potential food items in the leaf litter. Ant colonies exhibited nocturnal activity throughout the year, and they foraged significantly more intensively in the wet/warm (November–March) than in the cold/dry season (April–October). As the night begins, small groups of workers disperse and hunt individually on a wide diversity of litter arthropods of variable sizes. At dusk, encounters with foragers of the diurnal ponerine *Pachycondyla striata* Fr. Smith were conspicuously avoided by *O. chelifer*, which occasionally had their prey robbed by the former or were even taken as prey themselves. Termites were the preferred prey of *O. chelifer*, making up 40% of the food items captured in each season. Seasonal comparisons of prey organisms captured by *O. chelifer*, and of litter-dwelling arthropods sampled in pitfall traps, revealed that the frequency distribution of retrieved prey in each taxonomic group did not differ seasonally, despite the 2.7-fold increase in the overall availability of litter arthropods in the warm/wet period. This result supports foraging theory by showing that preference for certain animal prey types (i.e., taxonomic groups) persists through time despite seasonal fluctuations in the overall availability of potential prey on the forest floor. This study points out to the importance of studying ant foraging ecology and diet preferences in a natural context.

KEY WORDS   activity schedule, diet, ground-dwelling ants, ant behavior

The daily activity schedule is one of the most distinctive characteristics among species of ants (Hölldobler and Wilson 1990). Interspecific divergence in activity patterns result from particular morphological, physiological or behavioral traits that define the ecological tolerance of a species and thus determine its specific foraging period (Bernstein 1979). The temporal dimension of ant foraging behavior is constrained by several abiotic and biotic factors that might affect the costs of foraging and the use of time (Traniello 1989). Common abiotic factors affecting ant activity schedules include temperature (Cerdá et al. 1998) and moisture (Levings and Windsor 1984). Biotic factors such as interspecific competition (Carroll and Janzen 1973), natural enemies (Orr and Seike 1998), and variation in resource availability (Briese and Macauley 1980) also may influence activity patterns both on a daily and seasonal basis.

Ants in the subfamily Ponerinae often have small colonies with workers that exhibit solitary foraging (Peeters and Crewe 1987). Because ponerine ants are armed with a sting and many species have powerful mandibles, they are usually considered as predators.

Nonetheless, a diversity of feeding habits and foraging modes have been reported for members of this subfamily, which include hunting for food on ground and foliage substrates, scavenging for dead arthropods, gathering plant and insect exudates, and collecting fleshy fruit (Duncan and Crewe 1994, Déjean and Suzzoni 1997, Blüthgen et al. 2003, Oliveira and Freitas 2004, Dutra et al. 2006). In addition, although many ponerines feed opportunistically on a diversity of food types, some specialized species can be extremely specific in the kind of prey they consume (Freitas 1995, Leal and Oliveira 1995). Foraging strategies may range from solitary to cooperative hunting, with varying degrees of recruitment behavior among nestmates (Peeters and Crewe 1987).

Ant species in the genus *Odontomachus* are widely known by their trap-jaws used during hunting, which can instantaneously stun or kill prey, or during defense against natural enemies (Carlin and Gladstein 1989). When a potential prey contacts the trigger hairs of *Odontomachus*, the trap-jaws may close in <0.1 ms, resulting in a powerful mandible strike that has been considered an adaptation to feed on fast and soft-bodied arthropods (Spagna et al. 2008). Solitary foragers of *Odontomachus* are facultative termite-hunters

(Fowler 1980, Déjean and Bashingwa 1985) that also may feed on a wide range of invertebrate taxa (Ehmer and Hölldobler 1995) and also explore alternative resources such as insect honeydew (Carroll and Janzen 1973), extrafloral nectar (Blüthgen et al. 2003), and lipid- and protein-rich fleshy seeds and fruit (Pizo and Oliveira 2001, Passos and Oliveira 2003). Because availability of insect prey (Janzen and Schoener 1968) and plant-derived resources (Rico-Gray and Oliveira 2007) exploited by ants have a strong seasonal component, some ant species may change their foraging patterns and/or dietary preferences throughout the year to optimize food intake in accordance with colony phenology (e.g., Judd 2005).

The genus *Odontomachus* occurs widely in tropical and warm temperate regions and is especially abundant in the neotropics, ranging from semiarid environments to rain forests (Brown 2000). This article presents a detailed field account of the foraging ecology of the ant *Odontomachus chelifer* (Latreille) (Formicidae: Ponerinae), a widely distributed species in the Neotropical region that occurs in forest habitats from Mexico to Argentina (Kempf 1972). We provide qualitative and quantitative data on the natural history of *O. chelifer*, with emphasis on colony activity rhythms and dietary requirements across seasons in a forest reserve in southeastern Brazil. More specifically, we evaluate diet preferences in relation to the seasonal availability of potential food items in the environment.

Study Site and Methods. Fieldwork was carried out from August 1999 to July 2000 at the Santa Genebra forest reserve in Campinas, southeastern Brazil (22° 49′ S, 47° 06′ W; 670-m altitude). The vegetation consists of a semideciduous Atlantic forest fragment. The climate of the region exhibits considerable seasonal variation, with a warm/wet season lasting from November to March (highest mean monthly records: rainfall, 240.2 mm; temperature, 24.4°C) and a cold/dry season lasting from April to October (lowest mean monthly records: rainfall, 36.8 mm; temperature, 18.2°C) (Toniato et al. 1998).

Ten nests of *O. chelifer* were tagged in the forest for behavioral observations. Focal nests were 10 m off the main trail of the reserve and were at least 10 m away from one another. Food items were collected directly from the mandibles of returning foragers from any of the colonies. Prey items were preserved in 70% alcohol and brought to the laboratory for more detailed identification, and measurement of length. Total time spent sampling food items during cold/dry and warm/wet season was 21 and 18 h in each period, respectively.

Four nests were selected for data on colony activity schedule. We recorded all workers exiting or entering each nest within in a 24-h period. Samplings consisted of counting ants continuously during 40 min every 2 h. Ground temperature (depth $\approx$ 5 cm) around nest entrances was recorded four times at each 40-min session. The activity of each of the four colonies was measured once per season, in the cold/dry (June–August) and warm/wet (December–February) pe-

riod. To avoid disturbance of ant foragers, no food item was collected during sessions estimating the daily activity schedule of ant colonies. If possible, in such cases the food item was identified visually only.

Seasonal differences in the availability of potential prey consumed by *O. chelifer* was evaluated with 10 pitfall traps distributed on the ground in areas of thick leaf litter, along a 100-m transect in the forest. Traps were 10 m apart from one another, and were left open from 2000 to 2400 hours during three nonconsecutive nights in each season. Traps consisted of plastic bottles (10 cm in diameter) containing 200 ml of 70% ethanol solution.

Results

Nests of *O. chelifer* are located on the ground, with chambers and galleries extending among roots of adjacent trees. The single nest entrance measures $\approx$5 cm in diameter and is usually surrounded by a layer of humid leaf litter. Worker ants, winged forms, dealated queens, and immature stages can be found all the way down to $\approx$1.0 m below the soil surface.

O. chelifer exhibited a distinct nocturnal foraging activity throughout the year. The activity schedule is clearly influenced by the photoperiod (Fig. 1). Overall daily activity was negatively affected by ground temperature in the wet/warm season ($r_s = -0.65, P = 0.022$), but not in the dry/cold season ($r_s = -0.47, P = 0.12$). Seasonal variation in the activity of ant colonies was evident. During the warm/wet season the ants foraged intensively throughout the night, with few workers being observed outside their nests at daytime (Fig. 1A). However, in the cold/dry season colony foraging activity decreased markedly and very few ants were seen at night only (Fig. 1B).

Foragers of *O. chelifer* searched for food chiefly above and beneath the leaf litter, and only occasionally they were seen hunting on herbaceous vegetation. At sunset, small groups of workers were usually observed motionless at the nest entrance. As the night begins the ants disperse from these groups and forage individually in the midst of fallen leaves. As returning workers start bringing prey into the nest, ant departure from stationary groups at nest entrances tends to increase. As they search for food, foragers keep their trap-jaws open and frequently touch the substrate with the antennae. When a potential prey is found, the ant forager approaches cautiously and strikes with the mandibles. As a result the prey can be injured and the ant is usually thrown 10–15 cm backward. This behavioral sequence can be repeated many times before a live prey is entirely subdued. More resistant prey such as beetles were normally stung during struggle with *O. chelifer*. Ant foragers retrieved prey solitarily, and group hunting or cooperation during prey retrieval was never observed.

Foragers of *O. chelifer* preyed on a wide variety of live litter-dwelling arthropods and were also highly opportunistic in scavenging dead invertebrates (Fig. 2). *Neocapritermes* termites (Fig. 3A) were the most frequent prey, but they also preyed on other ants such
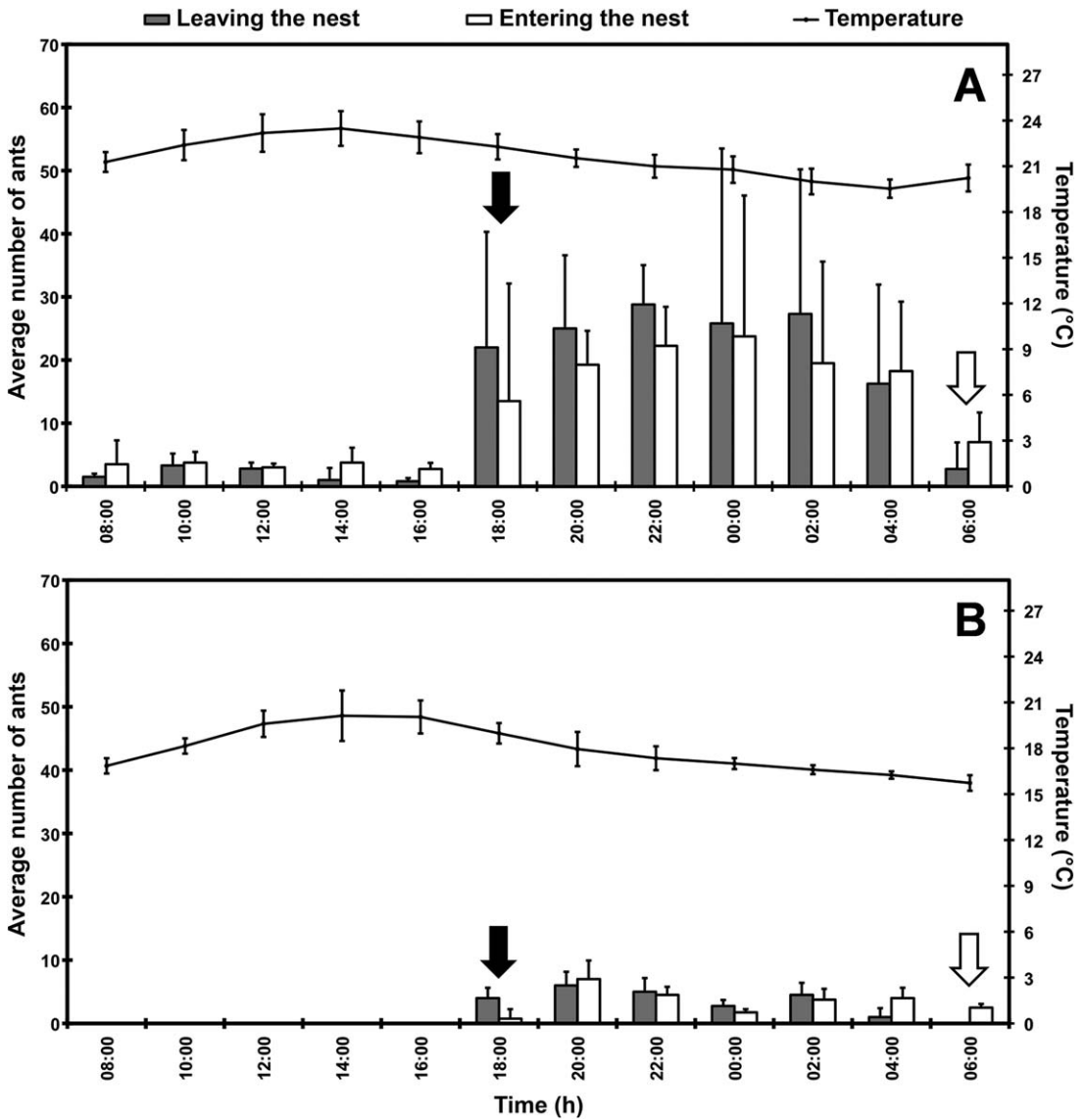
Fig. 1. Activity schedule of *O. chelifer* (bars) and ground temperature (solid line) in a forest reserve in southeastern Brazil in the warm/wet (A) and cold/dry season (B). The arrows indicate sunset (black) and sunrise (white). Four colonies were monitored each season. Data are means ± SD.

as leaf-cutters (*Atta sexdens* Forel, *Acromyrmex* sp.) and carpenter ants (*Camponotus* spp.), as well as adults and larvae of Coleoptera and Lepidoptera. Scavenged arthropod matter included honey bees, harvestmen and spiders. Occasionally, foraging ants also collected small portions of mammal feces and fragments of arthropods. Encounters with the large, diurnal ponerine *Pachycondyla striata* Fr. Smith was conspicuously avoided by *O. chelifer* foragers, which occasionally had their prey robbed by the former, or were even fiercely attacked and carried as prey themselves (Fig. 3B).

The data from the pitfall traps revealed a marked seasonal difference in the overall availability of ar-thropods in the forest ($G = 142.12$, df $= 1$, $P = 0.0001$). Indeed, over twice as many arthropods were sampled in the pitfall traps during the warm/wet season (458 individuals) compared with the cold/dry season (166 individuals; Fig. 2). The number of prey items retrieved by *O. chelifer* in each period was proportional to the total abundance of available prey, making up ≈17% of the individual arthropods sampled in the pitfalls each season (Fig. 2). Likewise, termites remained as the preferred prey in both seasons, making up 40% of the items captured in each period.

The comparison between seasons of prey organisms effectively captured by *O. chelifer*, and of potential
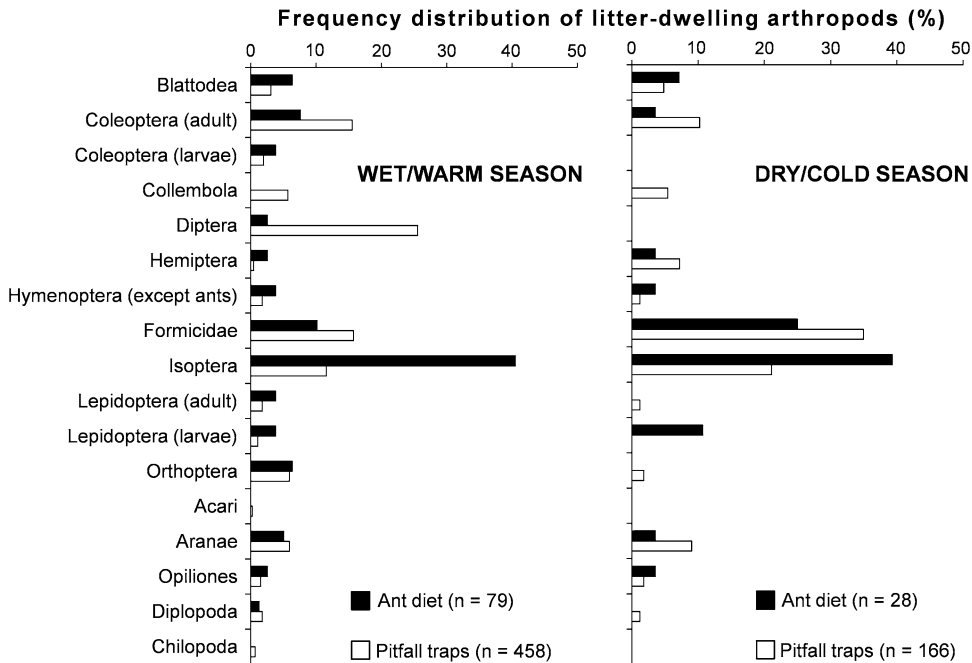
Fig. 2. Frequency distribution of different types of prey captured by *O. chelifer* foragers (10 focal colonies) and availability of litter arthropods sampled in pitfall traps in two seasons, in a forest reserve in southeastern Brazil. The frequency of prey items in each taxonomic group did not differ between seasons ($G = 13.80$, df = 16, $P = 0.61$). In the pitfall traps, the frequency of potential prey in each taxonomic group differed significantly between seasons ($G = 142.82$, df = 16, $P < 0.0001$). Despite seasonal variation in prey availability, however, ant foragers exhibited a similar general diet pattern in both periods, with a clear preference for termites. Note the 2.7-fold increase in the overall food availability in the wet/warm compared with the dry/cold season ($G = 142.12$, df = 1, $P = 0.0001$).

prey sampled in the pitfall traps (categorized in taxonomic groups), revealed a similar pattern of diet choice throughout the year, despite the 2.7-fold increase in the overall availability of litter arthropods in the warm/wet season (Fig. 2). The frequency distribution of prey items captured by *O. chelifer* in each taxonomic group did not differ between seasons ($G = 13.80$, df = 16, $P = 0.61$). In the pitfall traps, however, the frequency of potential prey in each taxonomic group differed significantly between seasons ($G = 142.82$, df = 16, $P < 0.0001$). This suggests that foragers of *O. chelifer* are consuming prey organisms irrespective of their abundance on the forest floor. For example, although the availability of dipterans increased markedly in the warm/wet season, these insects were poorly represented among the food items captured by the ants in that period. It is possible that a high fleeing capacity and physical or chemical defense of some taxa make them less vulnerable to *O. chelifer*. Termites remained as the preferred prey in both seasons, followed by ants (Fig. 2). Foragers of *O. chelifer* tended, however, to capture prey of larger size in the warm/wet season (mean ± SD = 6.8 ± 3.5 mm, range = 2.6–22.0 mm, n = 45) compared with the cold/dry period (mean ± SD = 4.7 ± 2.9 mm, range = 1.8–12.3 mm, n = 28) (t = 2.69, df = 71, P = 0.009).

Discussion

To grow and reproduce well, animals facing fluctuations in abiotic conditions must adjust their physiology, activity rhythms, and foraging behavior accordingly (Morse 1980). Temperature, moisture, and food availability are known to mediate daily and seasonal activity shifts in many insect groups (Heinrich 1993). Although ant colonies may behaviorally control micro environmental conditions, each species tend to function within a clear temperature–humidity range (Hölldobler and Wilson 1990).

Temperature is regarded as a central factor regulating ant activity (Cerdá et al. 1998). Among temperate species, soil temperature in particular has been shown to mediate colony activity schedule (e.g., Bernstein 1979) and may even influence the choice of nesting sites and territorial behavior (Sanada-Morimura et al. 2006). In our tropical forest site, the daily activity pattern of *O. chelifer* was associated with variation in ground temperature only in the hot period, when daytime temperatures in the forest are usually above 25°C (Medeiros and Oliveira 2009). However, contrary to *O. chelifer* that remains strictly nocturnal year-round (Fig. 1), some ant species may adjust their daily activity schedules in accordance with seasonal shifts in abiotic conditions. In the same forest site of the current study, colonies of obligate termitophagous
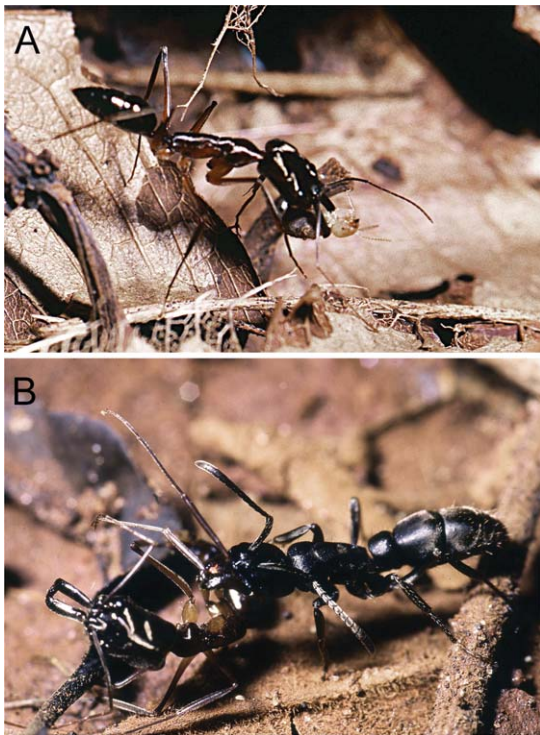
Fig. 3. (A) *O. chelifer* worker retrieving a termite prey on the leaf litter of a Brazilian forest. Termites comprise 37% of the prey items consumed by *O. chelifer*. (B) *P. striata* forager transports to its nest a recently-captured worker of *O. chelifer*. Aggressive interactions at dusk hours between the two species also may involve food robbing by *P. striata*. (Photographed by P.S.O.). (Online figure in color.)

Pachycondyla marginata (Roger) switch raiding activities to the night period in the hot season (Leal and Oliveira 1995). Similarly, severity of summer temperatures in arid Australia forces *Odontomachus* colonies to shift crepuscular activity in the spring toward nocturnal activity in the hot period (Briese and Macauley 1980). Maintenance of a nocturnal habit throughout the year by *O. chelifer* may be due in part to competitive interactions with diurnal foragers of *Pachycondyla striata* that also prey on litter arthropods, mostly termites and other ants (Medeiros and Oliveira 2009). In addition to intercepting laden workers of *O. chelifer* and robbing their prey, foragers of *P. striata* may actually prey on *O. chelifer* (Fig. 3B). Interspecific aggression near rich food resources (e.g., a large fruit or animal prey) occasionally occurs at dusk hours. Indeed, individual hunters of *P. striata* and *O. chelifer* clearly avoid each other in the leaf litter, and frequently change routes upon an imminent encounter (Medeiros and Oliveira 2009). Thus, it is reasonable to suppose that temporal segregation in foraging schedules would be advantageous for either species but mostly *O. chelifer,* apparently the weaker competitor and a potential prey as well (in which case one would expect an expansion of its activity schedule toward daytime in the absence of *P. striata*). A similar situation

is found in Barro Colorado Island (Panama) for foragers of *Ectatomma ruidum* Roger and *Ectatomma tuberculatum* (Olivier) that exploit similar food sources and whose segregated activity peaks are suggested to reduce competition (Pratt 1989; also see Carroll and Janzen 1973). In the same area, adjustments of foraging patterns as a result of hostile interactions among ants has been reported by Wirth et al. (2003) for *Atta colombica* (Guerin-Meneville), which switch to nocturnal foraging after aggression by *Camponotus* at daytime.

Because temperature is less severe and seasonal oscillations are less extreme in the tropics than in the temperate region, insect abundance is frequently mediated by moisture in tropical habitats (Janzen and Schoener 1968). For litter-dwelling organisms, including ground-nesting ants, high soil humidity is crucial in reducing desiccation risks and in maintaining microbe and invertebrate populations that shape litter foodwebs (Levings and Windsor 1984). Indeed, the activity patterns of ground-dwelling ant colonies in tropical forests suggest that they track locations and time periods with more adequate moisture levels and/or nutritional quality (Kaspari and Weiser 2000). The marked increase of foraging activity in the warm/wet season by *O. chelifer* colonies has already been reported for other tropical ponerines in savanna and forest ecosystems (Déjean and Lachaud 1994, Leal and Oliveira 1995, Medeiros and Oliveira 2009). This tendency follows the period of higher availability of potential litter-dwelling prey (Fig. 2) and is also associated with increased quantities of brood in *O. chelifer* colonies (Medeiros et al. 1992), which may require increased levels of protein intake by foragers (Judd 2005). Similar results were obtained for the arboreal ant *Gnamptogenys moelleri* (Forel) (Ectatomminae) in coastal sandy forest (Cogni and Oliveira 2004) and for *Camponotus sericeiventris* Guérin (Formicinae) in cerrado savanna (Yamamoto and Del-Claro 2008).

O. chelifer presented an opportunistic diet including a broad diversity of food items within a variable size range, similar to other reports of tropical forest-dwelling ponerines (Duncan and Crewe 1994, Ehmer and Hölldobler 1995, Fourcassié and Oliveira 2002, Medeiros and Oliveira 2009). Surprisingly, *O. chelifer* foragers were not observed retrieving plant-derived food to their nests. Although fallen fleshy fruit can be a common food item of *O. chelifer* in coastal forests (Pizo and Oliveira 2001, Passos and Oliveira 2004), they were not available at our forest site during this study. Moreover, the ants were never seen collecting plant- or insect-derived exudates (e.g., extrafloral nectar and hemipteran honeydew), and returning foragers with enlarged gasters were never recorded. Indeed, *O. chelifer* hunts chiefly on the ground, although foragers may occasionally climb on seedlings in the vicinity of the nest (Passos and Oliveira 2004).

Individual foragers of *O. chelifer* searched for food and retrieved prey without cooperation. This kind of foraging strategy can be efficient for species that exploit food items of variable size, which are distributed

in an unpredictable way in space and time (Fresneau 1985, Traniello 1989). The existence of stationary groups of *O. chelifer* workers at nest entrances has been considered a primitive recruitment mechanism by which forager departure increases as food is brought to the nest (Fowler 1980), and was also described for *Odontomachus bauri* (Oliveira and Höll-dobler 1989) and *O. ruginodis* (Carlin and Gladstein 1989).

The current field study supports foraging theory (Stephens and Krebs 1986) by showing that preference for certain animal prey types (i.e., taxonomic groups) by *O. chelifer* persists through time despite seasonal fluctuations in the overall availability of potential prey on the forest floor. Although diet spectrum includes a wide variety of arthropod taxa, termites remained as the preferred food throughout the year despite increased availability of other prey groups in the wet/warm period (also see Kuate et al. 2008). Although similar data are reported for species with specialized diets such as seed-harvesting ants (Crist and MacMahon 1992), this is one of the few field accounts of diet choice coupled with seasonal resource availability for an opportunistic, primarily carnivorous ant species (also see Yamamoto and Del-Claro 2008). Our results point out to the importance of studying ant foraging ecology and diet preferences in a natural context.

Foraging modes in ants are presumed to be the product of unique ecological pressures facing each species (Peeters and Crewe 1987). Indeed, distribution of food resources in size, time, space, and quality, as well as competitive interactions and predation risk, are regarded as the main ecological determinants of ant foraging strategies (Traniello 1989). Thus, a proper understanding of ant foraging ecology would require more field studies on general natural history of ants, including quantitative behavioral data associated with habitat structure, resource availability and diet preferences. In the complex tropical habitats, where ants are particularly abundant and diversified, basic ecological information of most species is clearly lacking.

Acknowledgments

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