

4 Season-Dependent Foraging Patterns

Case Study of a Neotropical Forest-Dwelling Ant

(Pachycondyla striata; Ponerinae)

Flávia N. S. Medeiros and Paulo S. Oliveira

CONTENTS

Introduction.....	81
Field Observations and General Procedure.....	82
Activity Patterns, Diet, and Foraging Behavior	82
Colony Home Ranges	83
Results.....	83
Nest Structure and Colony Demography	83
Activity Patterns.....	84
Diet, Behavior, and Foraging Modes	84
Colony Home Ranges	87
Aggressive Interactions.....	87
Discussion	89
Daily and Seasonal Activity Patterns	89
Diet and Foraging Modes.....	90
Colony Home Ranges and Aggressive Interactions	91
Concluding Remarks.....	92
Acknowledgments.....	92
References.....	92

INTRODUCTION

Ants are considered useful organisms to test hypotheses about foraging strategies because their foragers usually leave from a fixed nest site to collect food (e.g., Detrain and Deneubourg 2002). The development of models and hypotheses about ant foraging ecology, however, is constrained by the small amount of quantitative data on the foraging behavior of different ant taxa. The lack of data on the basic ecological features of ants is particularly evident in the Neotropical region, where these insects are extraordinarily abundant and diversified (Brown 2000).

Ants in the subfamily Ponerinae have retained many morphological and behavioral ancestral characteristics such as small colonies, simple nests, and solitary foraging (Peeters and Ito 2001). Because all members of the Ponerinae are armed with a sting and most species possess powerful

mandibles, they are usually considered predators. However, a variety of feeding habits and foraging strategies can be observed among species in this subfamily. For instance, ponerines may search for food both on the ground and on plant substrates, and they include species that scavenge for dead arthropods, gather plant and insect exudates, and collect fruits and seeds (e.g., Oliveira and Brandão 1991; Dejean and Lachaud 1994; Fewell et al. 1996; Rico-Gray and Oliveira 2007). Moreover, whereas many ponerine species feed opportunistically on an array of food items (Duncan and Crewe 1994; Ehmer and Hölldobler 1995; Fourcassié and Oliveira 2002), others are highly prey specific (Freitas 1995; Dejean and Evraerts 1997). The foraging modes are also highly variable among ponerine species, and may range from solitary hunting without any cooperation during search and food retrieval to different levels of cooperative foraging associated with varying degrees of recruitment behavior among colony members (Peeters and Crewe 1987).

The foraging activity of ant colonies can be affected by biotic (e.g., competition, natural enemies) and abiotic (e.g., temperature, humidity) factors, and may vary both on a daily and on a seasonal basis (e.g., Carroll and Janzen 1973; Bernstein 1975, 1979; Orivel and Dejean 2002; Philpott et al. 2004; Cogni and Oliveira 2004a). Ants in the ponerine genus *Pachycondyla* are found in warm temperate areas, but are more common in tropical and subtropical regions throughout the world (Brown 2000). The different species of *Pachycondyla* can nest both in soil and in vegetation, and most of them include a wide array of animal (dead and alive) and plant (liquid and solid) material in their diets (e.g., Fresneau 1985; Hölldobler 1985; Orivel et al. 2000). Some species, however, have taxonomically narrow diets, such as the specialized termite hunters (e.g., Leal and Oliveira 1995).

This chapter presents a detailed field account of the foraging ecology of the forest-dwelling ant *Pachycondyla striata*, aiming at an integration of individual and colony-level components of its foraging behavior (Traniello 1989). By hunting in a species-rich and unpredictable environment such as the leaf litter of tropical forests (Levings 1983; Ward 2000), the large *P. striata* foragers with their visible and easily identifiable prey seem ideal organisms to study foraging ecology on temporal and spatial scales as well as to illustrate patterns appearing in their foraging decisions. To study these aspects we provide qualitative and quantitative field data on diet and foraging modes, and analyze colony activity rhythms and home ranges in different seasonal contexts.

FIELD OBSERVATIONS AND GENERAL PROCEDURE

Fieldwork was carried out in the Santa Genebra Reserve at Campinas, Southeast Brazil (22°49'45"S, 47°06'33"W), where the climate is warm and wet, with a dry winter from April to October and a wet summer from November to March. The average annual rainfall is 1381.2 mm and the mean annual temperature is 21.6°C. Most of the reserve is covered by a semideciduous mesophytic forest (Raimundo et al. 2008).

ACTIVITY PATTERNS, DIET, AND FORAGING BEHAVIOR

A total of fifty nests of *Pachycondyla striata* were tagged in the study area by following loaded workers attracted to sardine baits. We monitored the activity rhythm of four of these colonies (>10 m apart from each other) by recording all workers exiting or entering each nest within 24 h. Samplings consisted of counting ants continuously during the first 20 min of every hour. Simultaneously, we recorded the air temperature and humidity. The activity of each of the four colonies was evaluated once per season (each colony on a different day) in the dry/cold (July) and rainy/wet (January) period.

The food items retrieved by *P. striata* were surveyed by removing them from the mandibles of returning foragers from any of the fifty nests tagged. This procedure allowed the compilation of

a large number of food items ($N = 132$). Foraging modes employed by workers of *P. striata* were determined by direct observation in the field and categorized as follows:

1. *Solitary scavenging*: Collection of dead organisms by a single worker.
2. *Group scavenging*: Collection of dead organisms by groups of two to five workers.
3. *Solitary predation*: Capture of live prey by a single worker.
4. *Predation in association with other ant species*: Capture of live termites in association with the obligate termitophagous ant, *Pachycondyla marginata* (see Leal and Oliveira 1995).
5. *Interspecific food robbing*: Stealing food from other ant species.

The food items taken from workers of *P. striata* were preserved in 70% alcohol and brought to the laboratory for their exact identification. The items were then kept in an oven at 60°C for 24 h, and their dry weights measured with a Mettler H51Ar analytical balance. In six cases the collection of the food item was not possible, yet they could be identified and were included in the survey and the respective foraging modes were documented.

COLONY HOME RANGES

To determine the foraging ranges of *P. striata* colonies, we monitored marked foragers of the same four colonies previously used for the investigation on activity rhythms. Sardine baits placed in the immediate vicinity of tagged nests induced ant foraging activity and allowed us to mark large numbers of workers from each colony. All individuals encountered outside the nests were then individually marked with dots of enamel paint (Testors Co., Rockford, Illinois) on the thorax and gaster, using a distinct color code for each colony. The foraging ranges of the colonies were assessed by following marked ants as they exited the nest and by recording the maximal distance they had walked before returning to the nest. Consecutively numbered flags were placed along a forager's route at approximately 1-min intervals. The maximal distances from the nest achieved by different ant foragers were measured, their directions determined with a compass, and the respective data points recorded on a map of the study plot. Maps of colony home ranges were then constructed based on the cumulative data of maximal distances achieved by the workers of each tagged colony. The foraging areas of the colonies were estimated as convex polygons created by connecting the outermost points at which workers were seen at intervals of 10° around a circumference with the nest entrance in the center. Colonies were monitored on nonconsecutive days during the dry/cold and rainy/hot season, mainly at the peak hours of their activity (see below). In total, nearly 60 h of observation per colony and season were carried out. Intra- and interspecific interactions involving *P. striata* were also documented during all field observation sessions.

To obtain data on nest structure and demography, four additional nests of *P. striata* were excavated. Ant voucher specimens are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil.

RESULTS

NEST STRUCTURE AND COLONY DEMOGRAPHY

Pachycondyla striata nests on the ground at shady sites, usually in close proximity to live trees and shrubs, under which the nest may extend among wooden roots. Although nests may have two to eight entrances beneath the leaf litter (20 to 80 cm apart from each other), most of the ant traffic occurs through a single main entrance. Excavated nests ($N = 4$) had five to six interconnected chambers located 5 to 80 cm beneath the ground surface. Pupae, large larvae, and winged females were found

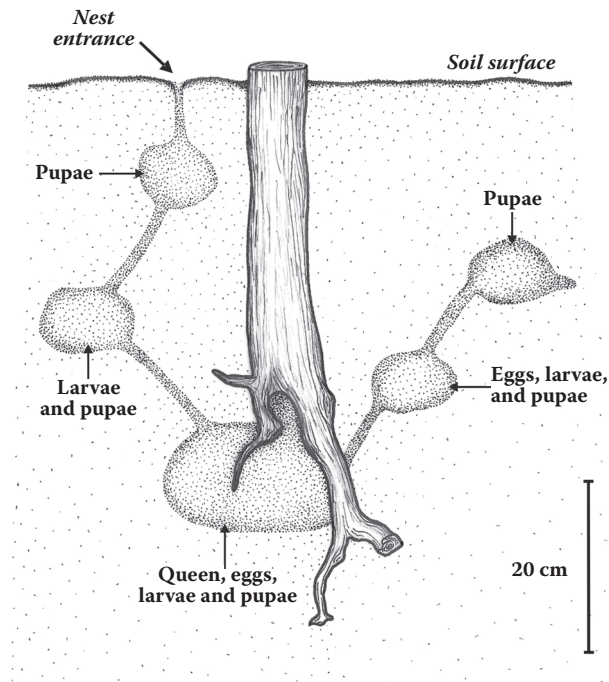


FIGURE 4.1 Vertical section through chambers and connecting galleries of a *Pachycondyla striata* nest next to the wooden roots of a live tree in a Brazilian forest. The profile is based on sketches from four excavated nests and shows their typical subterranean architecture during the rainy season when the brood is abundant.

in the more superficial chambers, whereas eggs, young larvae, and the queen were lodged in deeper chambers about 80 cm below the soil surface (Figure 4.1). The superficial chambers can be up to 1 m apart, suggesting a polydomous structure in which the colony is distributed in several spatial subunits.

The excavated *P. striata* colonies had one or no queen at all (so far, the occurrence of gamergates—mated, egg-laying workers—has not been documented in this species). The number of adult workers per colony ranged from 50 to 234 (145.5 ± 94.5 , mean \pm SD, $N = 4$). Immature stages (eggs, larvae, and pupae) were more abundant in the colonies excavated during the rainy/hot season (91 and 413, $N = 2$) than during the dry/cold season (15 and 20, $N = 2$).

ACTIVITY PATTERNS

In both seasons, the colony activity pattern was typically diurnal, with increased numbers of workers seen outside the nests at the warmest hours of the day (Figure 4.2). Worker activity was clearly lower in the dry/cold season than in the rainy/hot season. During winter, on average only up to two workers per sampling period (20 min of every hour) were seen during most of the day, with a slight increase in activity from 17.00 to 19.00 h, when air humidity increased and temperature was intermediate (Figure 4.2a). In contrast, during the summer, on average, at least four workers per sampling were seen outside the nest between 07.00 and 18.00 h, with a peak of activity from 11.00 to 17.00 h, when temperatures in the forest were usually above 25°C (Figure 4.2b).

DIET, BEHAVIOR, AND FORAGING MODES

Workers of *P. striata* forage for food mainly on the ground, above and beneath the leaf litter, and only occasionally climb on herbs to search for prey. Except for fast-moving ants and termites that are usually captured at once from behind (Figure 4.3a and b), potential prey organisms are

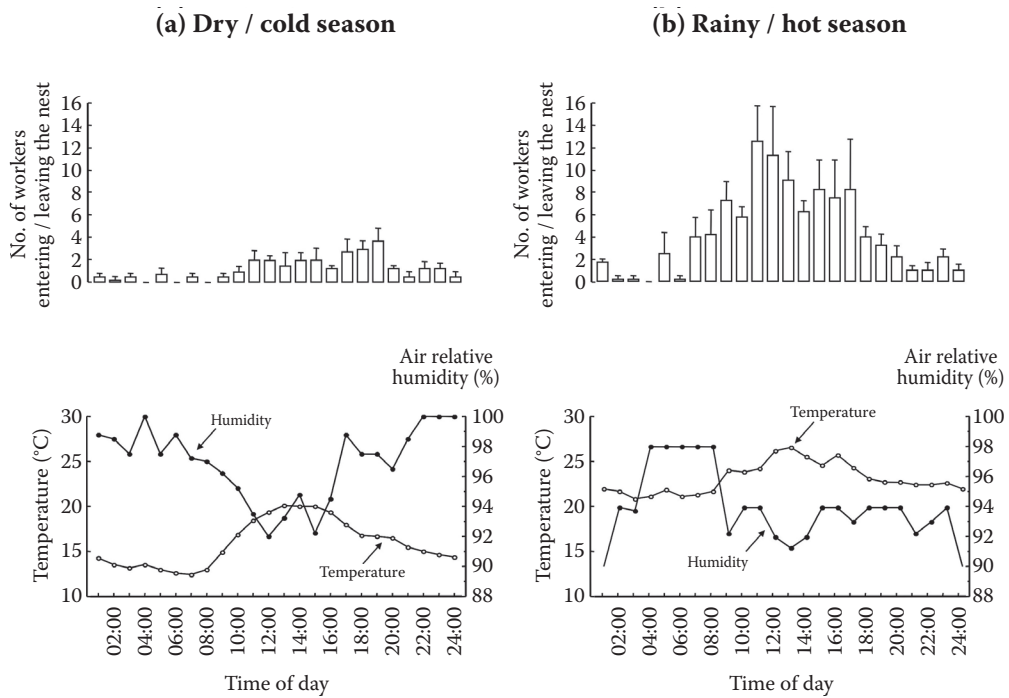


FIGURE 4.2 Daily and seasonal variation in the foraging activity of ground-dwelling *Pachycondyla striata* colonies in a Brazilian forest. The activity of four ant colonies was evaluated once during (a) the dry/cold season (July) and once during (b) the rainy/hot season (January). Bar graphs represent means (+1 SE; N = 4) of the colonies' foraging activity estimated as the number of workers entering or leaving the nest at a given time of the day. The temperature and humidity registered during the respective ant activity measurements are shown in the lower part of the figure.

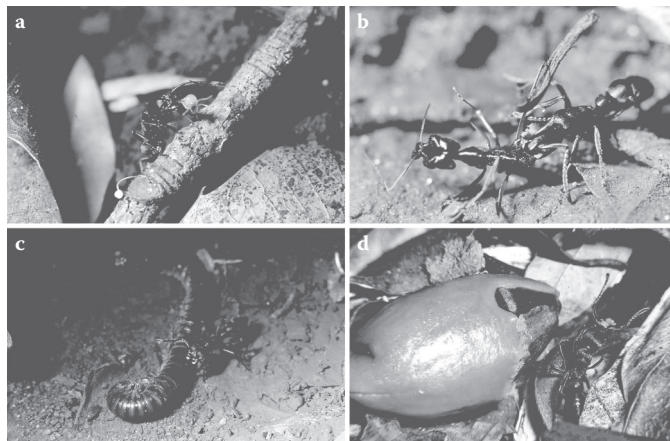


FIGURE 4.3 Photographs illustrating the variety of food items retrieved by *Pachycondyla striata* foragers on the leaf litter of a Brazilian forest. Individual hunters attack from behind small- to medium-sized ground-dwelling insects, such as *Neocapritermes* termites (a) and *Odontomachus* ants (b), and transport them to the nest. Large prey items, such as centipedes (c), usually require that the forager returns to the nest and recruits nestmates through tandem runs. (d) The fleshy portion of large fruits and seeds, such as the red lipid-rich aril of the *Virola* seed shown here, is sequentially retrieved in pieces by individual foragers. See color insert following page XXX. (Photographs by P. S. Oliveira (a, b, c) and M. A. Pizo (d).)

frequently inspected several times with the antennae before being attacked and retrieved by *P. striata* foragers. This latter behavior is commonly observed when the workers are confronted with large or well-armed prey items. From a total of 132 food items that were registered as part of the diet of *P. striata* in the study area, arthropods comprised the vast majority of the items retrieved by foraging ants (Figure 4.4a). Ants accounted for 32% of the prey items collected, including the following species: *Camponotus abdominalis*, *C. crassus*, *C. sericeiventris* (Formicinae), *Odontomachus chelifer*, *Pachycondyla marginata*, *P. striata*, *Pachycondyla* sp. (Ponerinae),

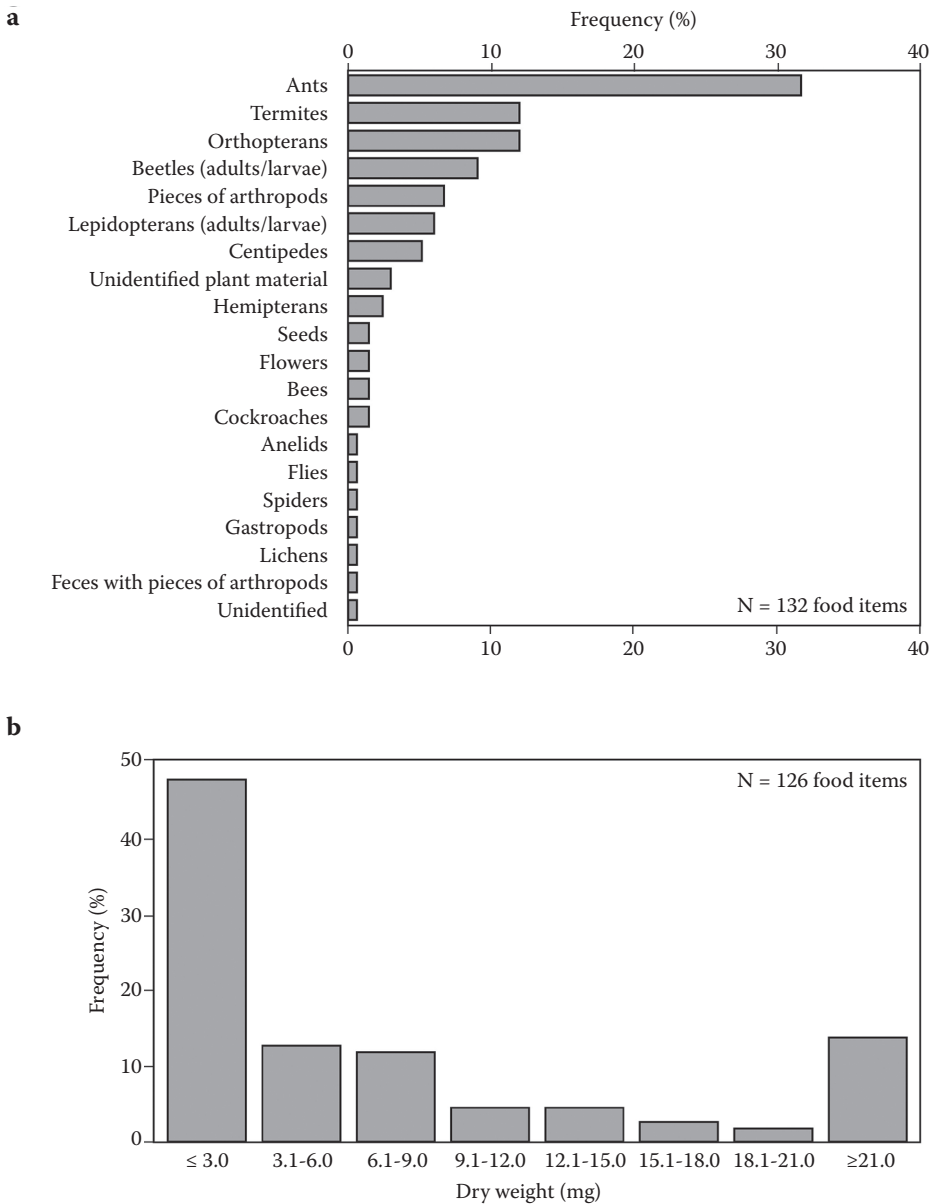


FIGURE 4.4 Relative abundance of the food items (a), and of their dry weights (b), that were retrieved by *Pachycondyla striata* foragers in a forest reserve in Brazil. Data are based on collections from returning ants of fifty observation nests.

Atta sexdens, *Pheidole* sp., and *Solenopsis* sp. (Myrmicinae). The vast majority (93%) of the ant prey consisted of dead workers, and only rarely did *P. striata* foragers kill other ants before retrieving them as food items (Figure 4.3b). Termites (workers, soldiers, and winged females) and orthopterans each accounted for 12% of the items captured by *P. striata*, followed by beetles (9%), parts of arthropods (7%), and lepidopterans (adults and larvae; 6%). Plant material, including fleshy fruits or seeds (Figure 4.3d) as well as flowers, and lichens accounted for only a small proportion of the food items sampled (Figure 4.4a). Nearly half of the food items retrieved by *P. striata* foragers consisted of insect parts or small insect prey such as ants and termites (dry weight ≤ 3.0 mg), whereas large arthropods such as katydids and centipedes (≥ 21.0 mg) accounted for ca. 14% of the ants' diet (Figures 4.3c and 4.4b).

Foragers of *P. striata* employ a variety of strategies to obtain food (Figure 4.5). The main feeding mode observed was scavenging for dead arthropods by solitary foragers, which accounted for 77% of the records in the field. In case the food item was too big to be carried by a single worker, solitary scouts usually returned to the nest in order to recruit other workers by means of tandem runs (observed in 5.5% of the cases). Predation on small- to medium-sized live arthropods by individual *P. striata* foragers comprised 10% of the feeding events seen in the field (Figure 4.5). Predation on termites was observed under two circumstances: First, individual *P. striata* foragers sometimes actively preyed on the winged sexuals during termite nuptial flights, as well as on workers and soldiers that aggregated in the vicinity of the nest entrances. In the second special case, *P. striata* joined raids on nests of *Neocapritermes opacus* (an abundant termite in the study area) performed by the specialized termitophagous ant *Pachycondyla marginata* (Leal and Oliveira 1995). In these cases, foragers of *P. striata* may take advantage of the intense excitement caused by the raid and enter the termite nest to capture workers, soldiers, or alates of *N. opacus*. Finally, interspecific food robbing was occasionally observed in *P. striata* foragers, which intercepted returning workers of other ant species such as *Odontomachus chelifer*, *Camponotus crassus*, and *Pheidole* sp., and robbed their insect prey, which included moths, beetle larvae, and winged ants (Figure 4.5).

COLONY HOME RANGES

The foraging home ranges of the four monitored *P. striata* colonies are shown in Figure 4.6. The maps are presented both separately for the dry/cold and rainy/hot seasons and overlapping in order to better illustrate seasonal variation in the colonies' foraging areas. The area used by the colonies to forage ranged from 1.5 m² (Colony I in the dry season) to 19.0 m² (Colony IV in the rainy season). Overall, home ranges tended to be larger in the rainy season than in the dry season (Mann-Whitney U test: $U = 15.5$; $P = 0.028$). The ants also considerably changed their foraging terrain during the different seasons. For instance, the foraging area of Colony III was not only larger in the rainy season but also rotated by nearly 180° compared to the home range observed in the dry period (Figure 4.6).

AGGRESSIVE INTERACTIONS

Foragers of *P. striata* were frequently engaged in intra- and interspecific combats with other ants at the border of their colony home ranges or in the vicinity of their nests. Such agonistic encounters sometimes lasted for more than 1 h, during which the ants usually bit and stung each other vigorously. In fights between non-nestmate *P. striata* foragers, the opponents frequently remained locked to one another for up to 30 min until one worker eventually killed or severely injured the rival, which was then carried to the nest as prey. *P. striata* ants with mutilated legs or antennae were commonly observed in the field, possibly as a result of such combats. Most of the fights seen in the field involved non-nestmate *P. striata* foragers, but dealated queens of *P. striata* that tried to intrude a foreign nest were also fiercely attacked by resident workers. Combats between *P. striata* and other

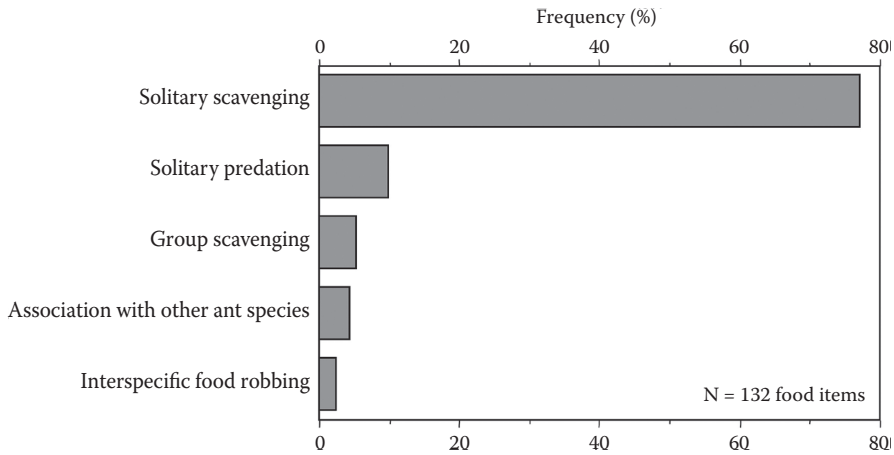


FIGURE 4.5 Frequency of occurrence of the various foraging modes employed by ground-dwelling *Pachycondyla striata* foragers in a Brazilian forest. Foraging techniques are defined as follows: *solitary scavenging*, retrieval of dead prey by a single forager; *group scavenging*, group retrieval of dead prey by two to five workers; *solitary predation*, capture of live prey by a single worker; *association with other ant species*, retrieval of live termites from their nests during raids by the termitophagous ant *Pachycondyla marginata*; and *interspecific food robbing*, theft of food from other ant species. Data are based on collections from returning foragers of fifty observation nests.

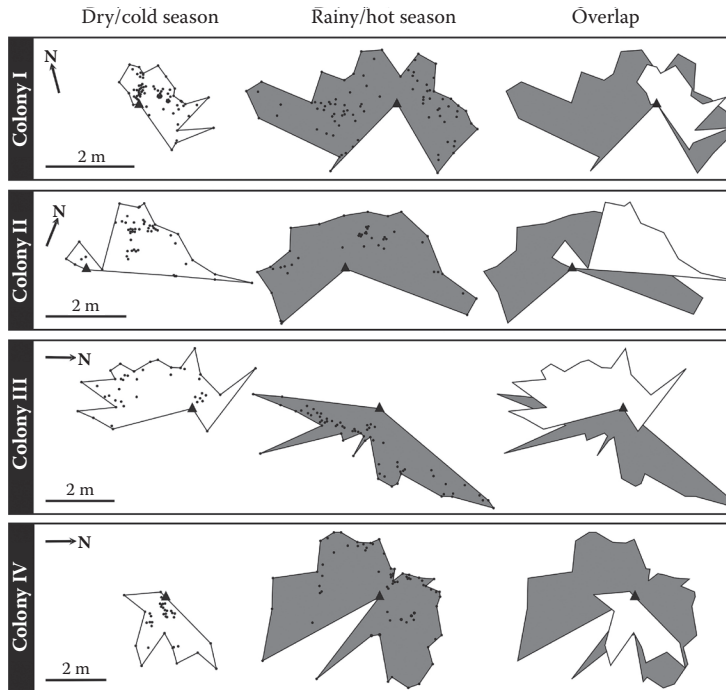


FIGURE 4.6 Seasonal variation of the home ranges of four *Pachycondyla striata* colonies in a forest reserve in Brazil. Maps are based on maximal distances achieved by individual foragers (represented by filled circles). The convex polygons for each colony were drawn by connecting the outermost points at which workers were seen, at intervals of 10° around the nest entrance (filled triangle). The home ranges of all four colonies were larger during the rainy/hot season (grey filled polygons) than during the cold/dry season (white polygons). Overlaps are shown to better illustrate the seasonal variation in the foraging areas of the colonies.

ant species involved *Pachycondyla marginata*, *Odontomachus chelifer*, and *Atta sexdens*. Pairwise interspecific aggression was usually observed near rich food resources (e.g., fallen fleshy fruits or large prey items), when the foraging paths of *P. striata* crossed that of other species, or during food robbing (see above). Foragers of *P. striata* and *O. chelifer* conspicuously avoided each other in the field, and frequently altered their routes in the imminence of an encounter. Finally, *P. striata* foragers themselves occasionally fell prey to other ant species that hunt cooperatively, as indicated by worker carcasses found on the refuse piles of *Pheidole* and *Solenopsis* ants.

DISCUSSION

DAILY AND SEASONAL ACTIVITY PATTERNS

Abiotic conditions such as temperature and moisture can fluctuate widely in many natural habitats. Animals facing these environmental oscillations developed mechanisms to track them, and adjust their physiology and behavior in order to grow and reproduce efficiently; as animals switch between survival and reproductive strategies, their foraging behavior changes as well (Morse 1980; Stephens and Krebs 1986). Indeed, daily and seasonal activity shifts have been documented in a diversity of insect groups and are mediated mostly by temperature, relative humidity or moisture, and food availability (Heinrich 1993). Among the ants, every species operates within a certain temperature-humidity range. The tolerance of foraging individuals, however, is far more restricted than that of the entire colony, which can control microenvironmental conditions by moving between nest compartments or by clustering/dispersing colony members (Hölldobler and Wilson 1990).

Whereas in temperate climates the seasonal cycle clearly varies between warm months with high food availability and cold months with low food availability (Bernstein 1975, 1979), in the tropics moisture can mediate seasonal fluctuations, which are less extreme than the temperate seasons, but often are associated with fluctuating insect abundance and activity as well (Janzen and Schoener 1968; Wolda 1988). For instance, comparisons of the activity of litter-dwelling ants along moisture gradients in a seasonal Panamanian rainforest revealed a positive correlation between moisture and the workers' activity, which, in addition, increased rapidly upon experimental watering during the dry season (Levings 1983). Moist litter not only provides a suitable microhabitat for ant colonies, but sustains populations of microbes and microfauna that structure the litter food web (Levings and Windsor 1984). Increased activity in wet periods and habitats suggests that ant colonies are tracking decreased desiccation risks, increased food availability, or a combination of both (Kaspari and Weiser 2000).

Temperature is considered to be the primary control of colony activity and metabolism in ants (e.g., Porter and Tschinkel 1993). In addition, foraging periods have been found to correlate with soil surface temperature in many ant species (Bernstein, 1979). Moreover, ground temperature has recently been shown to mediate the preference for nesting sites and territorial behavior in ants (Sanada-Morimura et al. 2006). Temperature appears to be more important than humidity in determining daily activity rhythms in *Pachycondyla striata*, since increased activity matched well high daytime temperatures (Figure 4.2). In contrast, the activity schedule of the Amazonian *Dinoponera gigantea* is negatively associated with temperature and follows a bimodal pattern in which most activity is confined to early morning and late afternoon, with a marked decline around midday (Fourcassié and Oliveira 2002). Such an activity pattern is commonly seen in warm environments, including sand dunes (Oliveira et al. 1999), savannas (Lévieux 1979), and deserts (Hölldobler 1976). It is also exhibited by other ponerine species living in tropical forests (Lévieux 1977; Dejean and Lachaud 1994; Duncan and Crewe 1994). *Pachycondyla striata* nests in shady sites and in close proximity to trees. The closed forest canopy and the thick leaf litter likely allow its colonies to keep midday activity in summer by buffering high temperatures in the understory or by keeping moderate levels of soil moisture.

Foraging activity by *Pachycondyla striata* varies markedly along the year. In the rainy/hot season more ants leave the nest to forage, and foragers travel longer distances than in the dry/cold season. Seasonal variation in foraging activity has already been reported in other tropical, forest-dwelling ponerines (e.g., Dejean and Lachaud 1994; Raimundo et al. 2008). However, whereas *Pachycondyla striata* remained strictly diurnal year-round, other ant species may switch their daily activity peak across seasons in order to adjust it to more appropriate temperature ranges in the course of the year (Hölldobler and Wilson 1990). For instance, in the nomadic and termitophagous *Pachycondyla marginata*, both hunting and migratory activities were strongly affected by seasonal factors, with a shift in foraging toward the night in the hot season (Leal and Oliveira 1995). Similarly, in arid Australia the activity of *Odontomachus* sp. depends on the temperature, and colonies switch from crepuscular activity in spring toward nocturnal activity in summer (Briese and Macauley 1980).

The increased foraging activity by *P. striata* during the rainy/hot season corresponds to the period of greater quantity of brood in the colonies and to a threefold increase in the abundance of potential litter-dwelling prey, as compared with the dry/cold season (Raimundo et al. 2008). Similar results were obtained with the bromeliad-nesting *Gnamptogenys moelleri* (Ectatomminae) in a coastal Brazilian forest (Cogni and Oliveira 2004a). Because changes in abiotic conditions may influence food availability and the colonies' phenology (Kaspari et al. 2001), environmental fluctuations should also affect a colony's food intake (e.g., Weeks et al. 2004; Judd 2005). Although we have not evaluated food intake by *P. striata* colonies across seasons, evidence from different groups of social insects indicates that food preference is correlated with the types of individuals being reared in the colony (West-Eberhard 1969; Michener 1974; Oster and Wilson 1978; Roubik 1989; Raveret Richter 2000). Because larvae are normally chief consumers of protein, their presence should increase protein intake by the colony (Stradling 1987; Weeks et al. 2004). Indeed, Stein et al. (1990) demonstrated that the imported fire ant, *Solenopsis invicta*, foraged for protein in warmer months when the colonies were reproducing, and for carbohydrates in colder months when the colony was in its growth stage (i.e., the period with a strong increase in worker number; Oster and Wilson 1978). Similarly, Judd (2005) showed that the highest preference for protein in spring and summer by *Pheidole ceres* correlated with an increased number of larvae within the colonies during this period.

DIET AND FORAGING MODES

Pachycondyla striata showed an opportunistic foraging behavior, with a flexible diet that included a wide array of live and dead invertebrates as well as plant matter within a variable size range (Figures 4.3 and 4.4). The taxonomic diversity of the food items in *P. striata*'s diet is similar to that documented for other ponerine species living in tropical forests (Fresneau 1985; Dejean et al. 1993; Duncan and Crewe 1994; Ehmer and Hölldobler 1995). Although ponerines have generally been regarded as primarily carnivorous ants, several studies have demonstrated that species in the genera *Pachycondyla*, *Odontomachus*, *Dinoponera*, and *Rhytidoponera* also consume lipid- and protein-rich fleshy parts of seeds and fruits to complement their diets (Horvitz and Beattie 1980; Davidson and Morton 1981; Pizo and Oliveira 1998; Fourcassié and Oliveira 2002; Passos and Oliveira 2002, 2004; Araújo and Rodrigues 2006).

In addition to a diversified diet, *P. striata* also employed a variety of foraging modes to retrieve food (Figure 4.5). Behavioral flexibility in hunting techniques involving individual and group retrieving of prey is well documented for other ant species, including ponerines and ectatommines (Peeters and Crewe 1987; Hölldobler 1984; Breed et al. 1987; Dejean et al. 1993; Schatz et al. 1997; Cogni and Oliveira 2004a, 2004b). As a generalist species, *P. striata* workers are frequently confronted with variable circumstances while hunting, and they take advantage of an array of foraging strategies to collect a large diversity of prey items. Interference competition with other foragers by taking food directly away from their mandibles is well known in ants and may involve both solid

and liquid food (Hölldobler 1986; Yamaguchi 1995; Richard et al. 2004). The technique employed by *P. striata* foragers consisted of stealing insect prey from returning workers of other ant species, which was also described for the African ponerine *Pachycondyla* (= *Hagensia*) *haviglandi* (Duncan and Crewe 1994). Although the theft of prey by gaining entry into other ant colonies (e.g., Breed et al. 1990) was not observed in *P. striata*, this species did join the obligate termitophagous ant *P. marginata* to enter raided termite nests in order to retrieve prey. This foraging mode is likely to be relevant for *P. striata* in the study area, because the preferred termite prey (*Neocapritermes opacus*) is locally very abundant (1 nest/3 m), and *P. marginata* colonies hunt for termites every 2–3 weeks (Leal and Oliveira 1995).

COLONY HOME RANGES AND AGGRESSIVE INTERACTIONS

The home ranges of animals change over time, and the largest shifts generally occur on a seasonal basis (Wittenberger 1981). Although daily and seasonal foraging activities are well documented in ants, little is known about temporal changes in their foraging home ranges (but see Gordon 1995). In an environment such as the forest floor, where the distribution of resources can vary widely in space and time (Levings 1983), continual sampling of adjacent areas should result in more efficient foraging than concentrating entirely on the location of the most recent successful foraging site (Stephens and Krebs 1986).

Our results show that *P. striata* colonies markedly change their home ranges across the seasons, considerably expanding or switching them in the rainy/hot season (Figure 4.6), when brood is abundant and more prey is available in the forest environment (Raimundo et al. 2008). Indeed, there is evidence that other ground-dwelling ants can also make significant adjustments to the directional and temporal aspects of their home range orientation. For instance, Gordon (1995) demonstrated that the foraging ranges of harvester ant colonies (*Pogonomyrmex barbatus*) differed significantly between subsequent years: only about half of a colony's foraging range in one summer had been used by this colony in the previous summer (Gordon 1995). Similarly, although home ranges of the African *Pachycondyla* (= *Brachyponera*) *senaarensis* are of the same size in the rainy and dry seasons, there is a marked shift of the hunting terrains exploited by the colonies across the seasons (Dejean and Lachaud 1994). In the Brazilian Atlantic forest, workers of the arboreal *Gnamptogenys moelleri* colonies foraged only on their nest bromeliads during winter, but considerably expanded their home ranges to the ground and neighboring shrubs and trees in the summer. At this time of the year the amount of brood in the colonies is increased, arthropod prey is abundant, and *Gnamptogenys* foragers are nearly three times more efficient in retrieving food than in the winter (Cogni and Oliveira 2004a). The home range aboveground of the African stink ant, *Pachycondyla* (= *Paltothyreus*) *tarsata*, is generally not greater than 5 m (Hölldobler 1984). However, underground trunk routes with multiple exit holes enable a colony to considerably expand its territory and to have foragers collecting food up to 40 m away from the main nest, thereby covering a foraging area of 1,200 m² (Lévieux 1965; Dejean et al. 1993; Braun et al. 1994). This decentralization of the foraging territories through subterranean pathways reduces both predation on foragers and aggressive interactions with competitors, and in addition, minimizes the desiccation risk for workers (Hölldobler and Wilson 1990; Dejean et al. 1993).

Resource availability, costs of defense, and life history may all interact to influence territory size in animals and, more broadly, the way they use space (Wittenberger 1981; Gordon 1995). Colonies of *P. striata* have relatively small foraging areas (1.5 to 19.0 m²), which is consistent with the home ranges of other forest-dwelling ponerines (Hölldobler 1984; Dejean et al. 1993; Duncan and Crewe 1994). The maintenance of a foraging area by *P. striata* colonies apparently is costly, since intra- and interspecific combats that can cause death or severe injury to foragers were frequently observed within their home ranges. Aggressive interactions with other ant species usually occurred near food sources and involved the theft of prey by *P. striata* and occasionally the death of the robbed ant. Similar observations were also reported for *Pachycondyla* (= *Hagensia*) *haviglandi* in

Africa (Duncan and Crewe 1994), and fierce territorial fights have been described for several other ant species (see Hölldobler and Wilson 1990). In some species, however, ritualized contests rarely cause death, probably because bites are aimed mostly at the mandibles, thorax, or legs rather than at vital spots such as joints or the gaster (e.g., Sanada-Morimura et al. 2006). In the Amazon forest, Fourcassié and Oliveira (2002) found that *Dinoponera gigantea* foragers from neighboring colonies may engage in ritualized contests at the border of their foraging areas (ca. 10 m around the nest) that can last up to 30 min, during which the ants usually faced each other frontally and locked their mandibles together. As opposed to *P. striata*, however, intraspecific contests in *Dinoponera* caused no apparent injury to either of the ants involved (Fourcassié and Oliveira 2002).

CONCLUDING REMARKS

Forest-dwelling *Pachycondyla striata* ants exhibit a highly flexible foraging behavior that comprises an array of prey hunting techniques, including individual and group scavenging, solitary predation, predation in association with other species, and food robbing. Such a diversity of foraging modes allows *P. striata* workers to feed on live and dead invertebrates as well as on plant matter within a broad size range. Moreover, this ant species adjusts its activity patterns and the size and orientation of its home ranges according to seasonal oscillations in its environment. It is not clear to what extent (if at all) intra- and interspecific aggression with other ants mediates shifts in the home range boundaries of *P. striata* colonies. This question remains open for future investigations.

As a generalist species facing variable and complex ecological settings in both space and time, *P. striata* represents a suitable model to evaluate the integration of individual- and colony-level components of the foraging system of ant colonies. The field study presented in this chapter illustrates how the combination of natural history information with quantitative behavioral data can link ecological factors with the observed foraging patterns and strategies of a social insect.

ACKNOWLEDGMENTS

We are grateful to Stefan Jarau and Michael Hrnecir for the invitation to contribute to this volume. A. V. Christianini, R. Cogni, A. V. L. Freitas, L. Kaminski, M. A. Pizo, P. Rodrigues, and M. Uehara-Prado provided helpful suggestions on the manuscript, and L. Kaminsky also assisted with the line drawings. S. Jarau and M. Hrnecir considerably improved the final version of the manuscript. We thank the staff of the Santa Genebra Reserve for logistic support, and several colleagues for help in the field. Financial support to FNSM was provided by CAPES, and to PSO by the Brazilian Research Council (CNPq).

REFERENCES

- Araújo A, Rodrigues Z. (2006). Foraging behavior of the queenless ant *Dinoponera quadriceps* Santschi (Hymenoptera: Formicidae). *Neotrop Entomol* 35:159–64.
- Bernstein RA. (1975). Foraging strategies of ants in response to variable food density. *Ecology* 56:213–19.
- Bernstein RA. (1979). Schedules of foraging activity in species of ants. *J Anim Ecol* 48:921–30.
- Braun U, Peeters C, Hölldobler B. (1994). The giant nests of the African stink ant *Paltothyreus tarsatus* (Formicidae, Ponerinae). *Biotropica* 26:308–11.
- Breed MD, Abel P, Bleuze TJ, Denton SE. (1990). Thievery, home ranges, and nestmate recognition in *Ectatomma ruidum*. *Oecologia* 84:117–21.
- Breed MD, Fewell JH, Moore AJ, Williams KR. (1987). Graded recruitment in a ponerine ant. *Behav Ecol Sociobiol* 20:407–11.
- Briese DT, Macauley BJ. (1980). Temporal structure of an ant community in semi-arid Australia. *Austral Ecol* 5:121–34.

- Brown WL. (2000). Diversity of ants. In Agosti D, Majer JD, Alonso LE, Schultz TR (eds.), *Ants: Standard Methods for Measuring and Monitoring Biodiversity*. Washington, DC: Smithsonian Institution Press, pp. 45–79.
- Carroll CR, Janzen DH. (1973). Ecology of foraging by ants. *Annu Rev Ecol Syst* 4:231–57.
- Cogni R, Oliveira PS. (2004a). Patterns in foraging and nesting ecology in the neotropical ant *Gnamptogenys moelleri* (Formicidae, Ponerinae). *Insect Soc* 51:123–30.
- Cogni R, Oliveira PS. (2004b). Recruitment behavior during foraging in the neotropical ant *Gnamptogenys moelleri* (Formicidae: Ponerinae): Does the type of food matter? *J Ins Behav* 17:443–58.
- Davidson DW, Morton SR. (1981). Myrmecochory in some plants (*F. chenopodiaceae*) of the Australian arid zone. *Oecologia* 50:357–66.
- Dejean A, Beugnon G, Lachaud JP. (1993). Spatial components of foraging behavior in an African ponerine ant, *Paltothyreus tarsatus*. *J Ins Behav* 6:271–85.
- Dejean A, Evraerts C. (1997). Predatory behavior in the genus *Leptogenys*: A comparative study. *J Ins Behav* 10:177–91.
- Dejean A, Lachaud JP. (1994). Ecology and behavior of the seed-eating ponerine ant *Brachyponera senaarensis* (Mayr). *Insect Soc* 41:191–210.
- Detrain C, Deneubourg JL. (2002). Complexity of environment and parsimony of decision rules in insect societies. *Biol Bull* 202:268–74.
- Duncan FD, Crewe RM. (1994). Field study on the foraging characteristics of a ponerine ant, *Hagensia havilandi* Forel. *Insect Soc* 41:85–98.
- Ehmer B, Hölldobler B. (1995). Foraging behavior of *Odontomachus bauri* on Barro Colorado Island, Panama. *Psyche* 102:215–24.
- Fewell JH, Harrison JF, Lighton JRB, Breed MD. (1996). Foraging energetics of the ant, *Paraponera clavata*. *Oecologia* 105:419–27.
- Fourcassié V, Oliveira PS. (2002). Foraging ecology of the giant Amazonian ant *Dinoponera gigantea* (Hymenoptera, Formicidae, Ponerinae): Activity schedule, diet, and spatial foraging patterns. *J Nat Hist* 36:2211–27.
- Freitas AVL. (1995). Nest relocation and prey specialization in the ant *Leptogenys propefalcigera* Roger (Formicidae: Ponerinae) in an urban area in southeastern Brazil. *Insect Soc* 42:453–56.
- Fresneau D. (1985). Individual foraging and path fidelity in a ponerine ant. *Insect Soc* 32:109–16.
- Gordon DM. (1995). The development of an ant colony's foraging range. *Anim Behav* 49:649–59.
- Heinrich B. (1993). *The Hot-Blooded Insects: Strategies and Mechanisms of Thermoregulation*. Cambridge, MA: Harvard University Press.
- Hölldobler B. (1976). Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. *Behav Ecol Sociobiol* 1:3–44.
- Hölldobler B. (1984). Communication during foraging and nest-relocation in the African stink ant, *Paltothyreus tarsatus* Fabr. (Hymenoptera, Formicidae, Ponerinae). *Z Tierpsychol* 65:40–52.
- Hölldobler B. (1985). Liquid food transmission and antennation signals in ponerine ants. *Israel J Entomol* 19: 89–99.
- Hölldobler B. (1986). Food robbing in ants, a form of interference competition. *Oecologia* 69:12–15.
- Hölldobler B, Wilson EO. (1990). *The Ants*. Cambridge, MA: Harvard University Press.
- Horvitz CC, Beattie AJ. (1980). Ant dispersal of *Calathea* (Marantaceae) by carnivorous Ponerines (Formicidae) in a tropical rain forest. *Am J Bot* 67:321–26.
- Janzen DH, Schoener TW. (1968). Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49:96–110.
- Judd TM. (2005). The effects of water, season, and colony composition on foraging preferences of *Pheidole ceres* (Hymenoptera: Formicidae). *J Ins Behav* 18:781–803.
- Kaspari M, Pickering J, Longino JT, Windsor D. (2001). The phenology of a Neotropical ant assemblage: Evidence for continuous and overlapping reproduction. *Behav Ecol Sociobiol* 50:382–90.
- Kaspari M, Weiser MD. (2000). Ant activity along moisture gradients in a Neotropical forest. *Biotropica* 32: 703–11.
- Leal IR, Oliveira PS. (1995). Behavioral ecology of the Neotropical termite-hunting ant *Pachycondyla (=Termitopone) marginata*: Colony founding, group raiding and migratory patterns. *Behav Ecol Sociobiol* 37:373–83.
- Lévieux J. (1965). Description de quelques nids de fourmis de Côte d'Ivoire (Hym.). *Bull Soc Entomol Fr* 70: 259–66.

- Lévieux J. (1977). La nutrition des fourmis tropicales. V. Éléments de synthèse. Les modes d'exploitation de la biocenose. *Insect Soc* 24:235–60.
- Lévieux J. (1979). La nutrition des fourmis granivores IV. Cycle d'activité et régime alimentaire de *Messor galla* et de *Messor* (= *Cratomyrmex*) *regalis* en saison des pluies fluctuations annuelles. Discussion. *Insect Soc* 26:279–94.
- Levings SC. (1983). Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: Some causes of patchy species distributions. *Ecol Monogr* 53:435–55.
- Levings SC, Windsor DM. (1984). Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. *Biotropica* 16:125–31.
- Michener CD. (1974). *The Social Behavior of the Bees: A Comparative Study*. Cambridge, MA: Harvard University Press.
- Morse DH. (1980). *Behavioral Mechanisms in Ecology*. Cambridge, MA: Harvard University Press.
- Oliveira PS, Brandão CRF. (1991). The ant community associated with extrafloral nectaries in the Brazilian cerrados. In Huxley CR, Cutler DF (eds.), *Ant-Plant Interactions*. Oxford: Oxford University Press, pp. 198–212.
- Oliveira PS, Rico-Gray V, Díaz-Castelazo C, Castillo-Guevara C. (1999). Interaction between ants, extrafloral nectaries, and insect herbivores in Neotropical coastal sand dunes: Herbivore deterrence by visiting ants increases fruit set in *Opuntia stricta* (Cactaceae). *Funct Ecol* 13:623–31.
- Orivel J, Dejean A. (2002). Ant activity rhythms in a pioneer vegetal formation of French Guiana (Hymenoptera: Formicidae). *Sociobiology* 39:65–76.
- Orivel J, Souchal A, Cerdan P, Dejean A. (2000). Prey capture behavior of the arboreal ponerine ant *Pachycondyla goeldii* (Hymenoptera: Formicidae). *Sociobiology* 35:131–40.
- Oster GF, Wilson EO. (1978). *Caste and Ecology in the Social Insects*. Princeton, NJ: Princeton University Press.
- Passos L, Oliveira PS. (2002). Ants affect the distribution and performance of *Clusia criuva* seedlings, a primarily bird-dispersed rainforest tree. *J Ecol* 90:517–28.
- Passos L, Oliveira PS. (2004). Interaction between ants and fruits of *Guapira opposita* (Nyctaginaceae) in a Brazilian sandy plain rainforest: Ant effects on seeds and seedlings. *Oecologia* 139:376–82.
- Peeters C, Crewe R. (1987). Foraging and recruitment in ponerine ants: Solitary hunting in the queenless *Ophthalmopone berthoudi* (Hymenoptera: Formicidae). *Psyche* 94:201–14.
- Peeters C, Ito F. (2001). Colony dispersal and the evolution of queen morphology in social Hymenoptera. *Annu Rev Entomol* 46:601–30.
- Philpott SM, Maldonado J, Vandermeer J, Perfecto I. (2004). Taking trophic cascades up a level: Behaviorally-modified effects of phorid flies on ants and ant prey in coffee agroecosystems. *Oikos* 105:141–47.
- Pizo MA, Oliveira PS. (1998). Interaction between ants and seeds of a nonmyrmecochorous neotropical tree, *Cabralea canjerana* (Meliaceae), in the Atlantic forest of Southeast Brazil. *Am J Bot* 85:669–74.
- Porter SD, Tschinkel WR. (1993). Fire ant thermal preferences: Behavioral control of growth and metabolism. *Behav Ecol Sociobiol* 32:321–29.
- Raimundo RLG, Freitas AVL, Oliveira PS. (2009). Activity schedule and diet of the ground-dwelling ant, *Odontomachus chelifer* (Formicidae: Ponerinae), in an Atlantic forest fragment. In preparation.
- Raveret Richter M. (2000). Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annu Rev Entomol* 45:121–50.
- Richard FJ, Dejean A, Lachaud JP. (2004). Sugary food robbing in ants: A case of temporal cleptobiosis. *CR Biol* 327:509–17.
- Rico-Gray V, Oliveira PS. (2007). *The Ecology and Evolution of Ant-Plant Interactions*. Chicago: University of Chicago Press.
- Roubik DW. (1989). *Ecology and Natural History of Tropical Bees*. Cambridge, MA: Cambridge University Press.
- Sanada-Morimura S, Satoh T, Obara Y. (2006). Territorial behavior and temperature preference for nesting sites in a pavement ant *Tetramorium tsushimae*. *Insect Soc* 53:141–48.
- Schatz B, Lachaud JP, Beugnon G. (1997). Graded recruitment and hunting strategies linked to prey weight and size in the ponerine ant *Ectatomma ruidum*. *Behav Ecol Sociobiol* 40:337–49.
- Stein MB, Thorvilson HG, Johnson JW. (1990). Seasonal-changes in bait preference by red imported fire ant, *Solenopsis invicta* (Hymenoptera, Formicidae). *Fla Entomol* 73:117–23.
- Stephens DW, Krebs JR. (1986). *Foraging Theory*. Princeton, NJ: Princeton University Press.
- Stradling DJ. (1987). Nutritional ecology of ants. In Slansky F, Rodriguez JG (eds.), *Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates*. New York: Wiley, pp. 927–69.

- Traniello JFA. (1989). Foraging strategies of ants. *Annu Rev Entomol* 34:191–210.
- Ward PS. (2000). Broad-scale patterns of diversity in leaf litter ant communities. In Agosti D, Majer JD, Alonso LE, Schultz TR (eds.), *Ants: Standard Methods for Measuring and Monitoring Biodiversity*. Washington, DC: Smithsonian Institution Press, pp. 99–121.
- Weeks RD, Wilson LT, Vinson SB, James WD. (2004). Flow of carbohydrates, lipids, and protein among colonies of polygynous red imported fire ants, *Solenopsis invicta* (Hymenoptera: Formicidae). *Ann Entomol Soc Am* 97:105–10.
- West-Eberhard M. (1969). The social biology of polistine wasps. *Misc Publ Mus Zool Univ Mich* 140:1–101.
- Wittenberger JF. (1981). *Animal Social Behavior*. Boston: Duxbury Press.
- Wolda H. (1988). Insect seasonality: Why? *Annu Rev Ecol Syst* 19:1–18.
- Yamaguchi T. (1995). Intraspecific competition through food robbing in the harvester ant, *Messor aciculatus* (Fr. Smith), and its consequences on colony survival. *Insect Soc* 42:89–101.