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A quantification of predation rates, indirect positive effects on plants, and foraging variation of the giant tropical ant, *Paraponera clavata*

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Abstract

While a clear consensus is emerging that predators can play a major role in shaping terrestrial communities, basic natural history observations and simple quantifications of predation rates in complex terrestrial systems are lacking. The potential indirect effect of a large predatory ant, *Paraponera clavata* Fabricius (Formicidae: Ponerinae), on herbivores was determined on rainforest trees at La Selva Biological Station in Costa Rica and Barro Colorado Island in Panama. Prey and other food brought back to nests by 75 colonies of *P. clavata* were quantified, taking into account temporal, seasonal, and microhabitat variation for both foraging activity and composition of foraging booty. The dispersion and density of ant colonies and combined density with the mean amounts of prey retrieval were used to calculate rates of predation per hectare in the two forests. In addition, herbivory was measured on trees containing *P. clavata* and on trees where the ants were not foraging. Colonies at La Selva brought back significantly more nectar plus prey than those at Barro Colorado Island, but foraging patterns were similar in the two forests. At both forests, the ants were more active at night, and there was no significant seasonal or colonial variation in consumption of nectar, composition of foraging booty, and overall activity of the colonies. At La Selva, trees containing *P. clavata* colonies had the same levels of folivory as nearest neighbor trees without *P. clavata* but had significantly lower folivory than randomly selected trees. Predation by this ant was high in both forests, despite its omnivorous diet. This insect predator is part of potentially important top-down controls in these wet and moist forests.

Keywords: La Selva, Costa Rica, Barro Colorado Island, Panama, foraging, predation, larvae, herbivory, indirect effects

Abbreviation:
BCI Barro Colorado Island
GIS Geographic Information Systems

Introduction

It has long been thought that predation is more intense in tropical compared to temperate ecosystems (Elton, 1973; Rathcke & Price, 1976; Gauld & Gaston, 1994). As a result, tropical herbivores might be expected to experience greater top-down control than temperate herbivores and top-down trophic cascades might be a common phenomenon (e.g., Dyer & Letourneau, 1999b). There are some data that support this hypothesis (Jeanne, 1979; Dyer & Coley, 2001) along with some indirect evidence, but very few appropriate comparisons have been made. The most cited indirect evidence that predation is more intense is that important predatory taxa are more diverse in the tropics. For example, most taxa of invertebrate predators, such as ants, are more species rich and abundant in tropical versus temperate systems (Fischer, 1960; Kusnezov, 1957; Wilson, 1971). However, many of these predators are probably omnivores and their diets may be primarily herbivorous. Actual quantification of numbers of prey along with other resources consumed by specific invertebrate predators in unmanipulated systems is rare (Finnegan, 1974; Cherix & Bourne, 1980; Hölldobler & Wilson, 1990; Jeanne, 1979; Dyer & Coley, 2001; Shelly, 1986 and references therein). Furthermore, levels of predation by different predators, either from the same or different species, exhibit significant variation (Hölldobler & Wilson, 1990; Dyer, 1997; Dyer & Bowers, 1996). Thus, many of the studies that have quantified levels of predation by single ant colonies (Wetterer, 1994) or in localized systems (e.g., Agrawal & Dubin-Thaler, 1999; Dyer & Letourneau, 1999a) may be misleading. In contrast to the less variable levels of mortality inflicted by specialist predators and parasitoids, this variation in response of generalist predators may also lessen the impact of individual predators on herbivory.

The giant tropical ant, *Paraponera clavata*, is a good

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candidate for quantifying predation and examining regional variation because of its large size, abundance in forests where it is found, and predatory effectiveness when compared to other invertebrate predators (Dyer, 1997). This ponerine ant is found in lowland tropical rainforests from Nicaragua to the central Amazon (Janzen & Carroll, 1983) and has been assigned to various feeding guilds including generalist predator (Wilson, 1971), opportunistic nectarivore (Hermann, 1975; Young, 1977), herbivore (Breed & Bennett, 1985), and scavenger (Janzen & Carroll, 1983; Young & Hermann, 1980). *Paraponera clavata* actively forages both in the understory and canopy. The ants make nests at the bases of trees, or up to 30 m on the bole of the tree, and have steady foraging trails on these and adjacent trees. Colony sizes at La Selva vary within 200-3000 adult workers (Breed and Harrison1988a; Janzen & Carroll, 1983; personal observations). When provided with prey, the ants readily take invertebrates (Dyer & Floyd, 1993; Dyer, 1995), and some vertebrates (Fritz *et al.*, 1981), and are not as discriminating as insects in two other predatory guilds (Dyer, 1997). Foraging studies have also indicated that *P. clavata* is primarily nocturnal (McCluskey & Brown, 1972), but this may vary between colonies (Hölldobler & Wilson, 1990).

The focus on experimental data in ecology has resulted in a reduction of correlative or descriptive studies that uncover broad patterns or measure important community variables, yet these patterns and variables are the basis for good theory and put experimental results into an appropriate context. The primary goal of this study was descriptive – characterizing predation in an unmanipulated tropical system. Observations were combined with correlational work and experiments to address the following questions: 1) What are predation rates of a common and important tropical predator, *P. clavata*? 2) What is the proportion of prey versus other components of this predator's diet? 3) How locally and regionally variable are the levels of predation? 4) How do these levels of predation on herbivores affect patterns of herbivory of tree leaves?

Methods

Study sites

P. clavata colonies were studied in two tropical forests. The first site, La Selva Biological Station, is a 1,516 ha wet forest operated by the Organization for Tropical Studies. Located in Heredia Province in northeastern Costa Rica (10°25' N 84°05' W) at 37 to 150m elevation, La Selva receives ~4200mm of rainfall annually and has a mild dry season that lasts only two months, with no month of the year averaging less than 100mm of rain (Sanford *et al.*, 1994). The second site, Barro Colorado Island (BCI; 9°10' N, 79°51' W), is a 1500 ha moist forest on an island in Lake Gatun, Panama, operated by the Smithsonian Tropical Research Institute. BCI has a mean altitude of 137m, receives 2600mm of rainfall annually with one dry season that typically lasts from mid-December until the end of April (Windsor, 1990).

At BCI 23 different colonies were studied in June and July, 1997. The colonies were randomly chosen from all marked colonies on the island. The density of *P. clavata* nests at BCI was 6.2 nests per hectare (Perez *et al.*, 1999). At La Selva, 52 different colonies were studied that were located either in the Holdridge Arboretum or in the forest adjacent to the first 3 km of what is now called the Sendero Tres Rios trail (the trail did not exist when the study was conducted). All colonies that were easily found in the two areas were used and observations were made during the following time periods: August 1 - 8, 1991; January 1 - 30, 1992; December 12, 1992 - January 20, 1993; and May 15 - July 9, 1993. The understory in the arboretum was regularly cut, but the ants were still found foraging along the ground. Eighteen of the 52 colonies were located in the arboretum, where there is no surrounding understory; the other colonies were in the forest. For both forests, all colony trees were medium to large, with a diameter of at least 10 cm.

Hereafter, the December/January periods are termed "dry" and the May - August periods "wet." Wet seasons on the Caribbean slope, where La Selva is located, generally begin in May and continue until December, or even mid-January. They are characterized by sunny mornings followed by very rainy afternoons and evenings. Dry seasons at La Selva are characterized by dry, sunny days interspersed with occasional rainy evenings and days. While a typical dry season at La Selva doesn't start until mid-January or February, both of the dry seasons in this study were normal (see Sanford et al., 1994, for a complete description of weather patterns at La Selva).

Booty analysis

During the 1993 wet season at La Selva and the 1997 wet season at BCI, one hour counts of ants emerging and returning to nests were conducted at 12 of the 23 BCI colonies and 13 of the 52 La Selva colonies at least twice during each of the following time periods: 1800 - 0200 (night), 0500 - 1000 (morning), and 1100 - 1800 (afternoon). For nine of the colonies at La Selva, counts were conducted every four hours in both the dry and wet seasons of 1993. For each returning ant, the item carried by the ant was recorded. It is well known that ponerine ants generally do not carry booty back to their nests in the crop (Hölldobler & Wilson, 1990), and during extensive observations in nectary experiments (Dyer, 1995), it was clear that ants returning from artificial nectar sources always carried visible drops of liquid between their mandibles. Likewise, ants returning with prey from predation experiments (Dyer, 1995) carried visible animal pieces in their mandibles. I therefore assumed that ants with empty mandibles were carrying nothing back to the nest. Counts were never conducted in heavy rain. After all the counts were conducted at La Selva, prey was collected from 30 ants from each of the 13 colonies in July 1993. These items were weighed to calculate average prey consumption rates (in mass) per colony.

Foraging observations and measure of selectivity

To determine prey acceptability simple foraging observations were made at La Selva in conjunction with previously published predation experiments (Dyer & Floyd, 1993; Dyer, 1995). These earlier experiments were conducted from 1991 to 1993 using all 52 colonies examined in the current study and also with solitary foraging ants found along trails and in the understory at La Selva. Dyer and Floyd (1993) and Dyer (1995) offered 909 lepidopteran larvae, of 108 species, to *P. clavata* foragers along their foraging trails (not including the solitary foragers) and observed predator and prey responses. To compare predation at the two sites, the same experiments and observations were conducted at BCI in June and July, 1997. 120 lepidopteran larvae were offered to the 23 BCI ant colonies and responses were recorded as described in Dyer and Floyd

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(1993). As many different species of larvae as possible were offered to mimic the diversity of larvae offered in the La Selva experiments; 10-15 individuals per species were offered randomly to the different colonies, and each colony was offered at least 5 caterpillars. The prey offered included 11 species in 11 families at BCI that were a subset of families offered at La Selva: Arctiidae, Geometridae, Hesperiidae, Megalopygidae, Noctuidae, Notodontidae, Nymphalidae, Papilionidae, Pyralidae, Saturniidae, and Sphingidae. For both sites, I recorded the number of ants rejecting individual larvae and the amount of time it took ants to subdue each one. Larvae were exposed to at least 10 individual ants before being recorded as completely rejected.

Density and distribution of ant nests at La Selva

Sixty points on the trail system at La Selva were randomly selected using a Geographic Information System (GIS). Each point was used to locate a rectangular plot of length 100 m and width 4 m. The plot length was perpendicular to the trail and the width was 2 m on either side of the GIS selected point. The direction leaving the trail (left or right) was chosen by the toss of a coin, unless there was only one direction that allowed for a 100 m plot. From February to April, 2001, each plot was carefully examined for one hour and the number of active *P. clavata* nests was recorded. Activity was confirmed by presence of foraging ants or by inserting a stick into the nest entrance to elicit defensive behavior by ants. The distinctive entrances of *P. clavata* nests were easily recognized. Mean density per m^2 was calculated and counts were statistically compared to a Poisson distribution to categorize the distribution of ants as random, clumped, or uniform.

Effects of ants on herbivory

From June – August, 1999, herbivory on trees containing *P. clavata* nests at the base of the trunk and foraging ants on the leaves was compared to herbivory on trees lacking these features. *Paraponera clavata* foraging is not confined to trees that harbor nests, but at La Selva foraging is most intense on nest trees (personal observations). Fourteen of the 52 La Selva colonies were randomly chosen for herbivory measurements. Control trees were the nearest neighbor trees of comparable size that contained no foraging ants. Due to logistical constraints, other species of invertebrate predators that may have been present (including other species of ants) on the control trees could not be determined. Fifteen newly expanded leaves that were at least 1 meter apart from each other were randomly chosen and the size and percent herbivory were measured using a plastic overlay with 1.5 X 1.5 cm grid. It is possible that the nearest neighbor trees were indirectly affected by the close proximity of foraging ants. Therefore, herbivory was measured again in January 2002, using the same ant trees and 14 randomly selected trees (each of which was at the beginning of the first 14 density plots described above). All leaves collected were close to the ground (2-5 m) for ease of sampling, and none of the tree pairs were the same species.

Statistical analyses

After appropriate tests of assumptions, univariate analysis of variance (ANOVA) was used to compare ant activity (measured as number of ants emerging) at BCI versus La Selva. Two Multivariate ANOVAs were also used to examine variation in foraging: 1) forest (La Selva, BCI) and time (morning, afternoon, night) were independent variables, and dependent variables were number of ants returning with prey and number returning with nectar, 2) for the 9 colonies at La Selva examined in both the dry and wet season, the independent variable was season (wet, dry) and dependent variables were prey and nectar. Profile analysis (Tabachnick & Fidell, 1996) was used to test parallel profiles for the numbers of ants with nectar versus prey. The parallel profiles test compares the dependent variable patterns of highs and lows for the various levels of the independent variables. For example, if ants return with more nectar in the evening versus other times, do ants also return with more prey in the evening versus other times? For hypothesis tests, the Wilks' Lambda statistic was used. The Index of dispersion test (Krebs, 1999) was used to compare the distribution of ants to a Poisson distribution. Percent herbivory on *P. clavata* versus control trees was compared using a paired t-test; herbivory on ant trees versus randomly selected trees was compared using a t-test. All measures of dispersion reported in the results are one standard error.

Results

Foraging observations

At La Selva the ants completely rejected 24.5% of the 909 offered larvae (Dyer & Floyd, 1993; Dyer, 1995), while in the current experiment at BCI, the ants rejected only 4.2% of 120 larvae. A typical predation event consisted of an individual ant sensing the prey, quickly pouncing on it, then taking the larva in its mandibles and repeatedly stinging it. The ants often grabbed the larva on the dorsal, anterior portion of the pronotum, making it difficult or impossible for it to bite the ant. The mean time it took an ant to subdue a larva was 180.9 seconds and varied from 7 seconds to over 1.5 hours (n = 1029 for both forests). Larvae varied in size from 7 mg to 8900 mg. There was a positive correlation between larval size and time required to subdue prey ($r = 0.13$, $P = 0.002$, $n = 1029$). This was much weaker than the correlation reported for another ponerine ant, *Ectatomma ruidum* (Schatz et al., 1997). If the prey was smaller and easy to subdue, the ant manipulated it into a manageable package and quickly carried it back into the nest. For larger prey, the ants utilized teamwork (*sensu* Franks, 1986) and often spread-eagled the prey (*sensu* Richard *et al*., 2001; Dejean *et al*., 2001). The ant would first attempt to subdue the larva, and then either return to the foraging trail to recruit other ants or wait until other ants found them. When larger larvae were offered to solitary foraging ants, the ants either rejected them or were able to subdue them and bring a part back to the nest before recruiting. Remains of larvae were always eventually brought to the nest, regardless of distance (n = 1029 for both forests, distances varied from 0.5 – 10 m from the nest entrance).

Booty analysis

The mean number of ants emerging per nest was not significantly different between forests ($F_{[1,98]} = 0.5$, $P = 0.5$, Table 1). There were significant differences in the mean amount of prey plus nectar returned to nests by ants for the two forests ($F_{[2,93]} = 4.3$, $P = 0.02$, Table 1), and the three times of day ($F_{[4,93]} = 6.0$, $P = 0.0001$), but there was no forest by time interaction ($F_{[4,93]} = 0.1$, P =

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Foraging item	LS	SE	BCI	SE
Ants Emerging	64.1	± 7.37	75	± 16.5
Ants Returning	77.3	± 15.4	82.8	± 20.7
Nectar	0.50	± 0.52	0.46	± 0.55
Nothing	0.29	± 0.22	0.38	± 0.29
Nest materials	0.094	± 0.092	0.058	± 0.04
Total prey	0.093	± 0.069	0.036	± 0.04
Atta cephalotes	0.053	± 0.057	unknown	
Lepidopteran larvae	0.028	± 0.02	0.005	± 0.009
Unsure	0.021	± 0.34	0.073	± 0.075

Table 1. Mean (± 1 SE) number of *Paraponera clavata* emerging and returning per hour, and mean proportion of items returned (e.g., an average of 50% of ants at La Selva nests returned with nectar). Means are based on 13 colonies at La Selva Biological Station (LS) and 12 colonies at Barro Colorado Island (BCI). "Total prey" includes lepidopteran larvae and *Atta*.

1.0). Ants from colonies at La Selva brought back more prey plus nectar than ants at BCI (Table 1). While it appears that this difference was due to a greater number of prey at La Selva rather than nectar (Table 1), the profile analysis indicated that there was no significant difference in the prey versus nectar response to forest ($F_{[1,93]} = 0.07$, $P = 0.8$). The profile analysis also revealed that the time effect was driven entirely by the nectar variable ($F_{[2,93]} = 12.4$, $P < 0.0001$), as ants at both BCI and La Selva returned with nectar most frequently in the evening (78.2 ± 16.2 ants returning with nectar and 6.5 ± 1.3 with prey per colony per hour) compared to the morning (29.0 ± 6.4 nectar ants and 4.9 ± 1.6 prey) and afternoon (8.2 ± 3.0 nectar ants and 5.5 ± 1.1 prey). For the 9 colonies at La Selva studied during both seasons, the overall MANOVA revealed no significant season effect on nectar and prey foraging ($F_{[2,46]} = 0.5$, $P = 0.6$), and the profile analysis indicated that there was no significant difference in the response of prey versus nectar ($F_{[2,46]} = 1.1$, $P = 0.3$). The average wet mass of prey items at La Selva was 0.13 ± 0.006 g. Most of these items were not entire organisms, so this value does not reflect the size of prey at the time of capture. As noted above, the ants process prey into manageable sizes.

At BCI, ants returning to their nests (total n = 11,052) most frequently carried nectar, followed by nothing, nest materials, and prey (Table 1). The most common prey or scavenged materials brought back were arthropods (90%), which were almost all adult hymenopterans (76% of arthropods) and immature lepidopterans (13% of arthropods). The percent of hymenopterans that were ants was not recorded. At La Selva, ants returning to their nests (total n = 27,720) most frequently carried nectar, followed by nothing, prey, and nest materials (Table 1). The most common prey or scavenged materials brought back were arthropods (98%), including hymenopterans (57% of arthropods were *Atta cephalotes* Linnaeus), lepidopteran larvae (30% of arthropods), and orthopterans (5% of arthropods). Because counts were conducted at the nest entrance, and not in the canopy where most foraging occurs, it was not possible to determine particulars of predation events such as where *A. cephalotes* were captured or what proportion of encountered individuals were killed. However, close inspection of all colony trees used for the booty analysis revealed that there was no visible damage on these trees from *A. cephalotes*.

Density and distribution of ant nests at La Selva and effects on herbivory

Mean density of nests at La Selva was 0.0018 ± 0.00045 per m^2 in the randomly selected plots, which is equivalent to 18 ± 4.5 per hectare, compared to 6.2 nests per hectare reported for BCI (Perez *et al.*, 1999). Both of these numbers are slight underestimates because they may have missed arboreal nests. The proportion of colonies that make arboreal nests is unknown, but it is likely to be as low as 5% (Breed and Harrison, 1988b; personal observations). The *P. clavata* nests had a clumped distribution, with an index of dispersion of 6.8 ($\chi^2 = 399.4$, DF = 59, $P < 0.0001$), unlike the uniform distributions found by Bennett and Breed (1985) in the arboretum at La Selva and by Perez *et al.* (1999) at BCI. The La Selva study is not inconsistent with these results, since the scale is very different (i.e. nests could be uniformly dispersed in the arboretum at La Selva, but clumped at the larger scale of the entire station). Combining these densities with number of prey returned per day and mean mass of prey items, the predation rate for *P. clavata* was 402.4 ± 0.7 g ha^{-1} d^{-1} at La Selva and 56.5 ± 0.1 g ha^{-1} d^{-1} at BCI (assuming that *P. clavata* prey have the same mass at that forest). Similarly, combining these densities with counts of specific prey items at La Selva, the direct effect of ants on herbivores was 1753.9 ± 95 *Atta cephalotes* ha^{-1} d^{-1} consumed and 925.7 ± 33.9 lepidopteran larvae ha^{-1} d^{-1} consumed.

Leaves from trees at La Selva with ants had 9.5% ± 1.9% herbivory which was not significantly less than nearest neighbor control trees (14.5% ± 2.9%; paired $t_{13} = -1.2$, $P = 0.25$), but subsequent comparisons revealed a significant (but still small) difference between ant trees (9.6% ± 1.3%) and randomly selected control trees (15.3% ± 2.4%; $t_{26} = -2.0$, $P = 0.05$). All these values fall within the 0.5% – 25.5% range of mean herbivory measured for plant species at La Selva (Marquis and Braker, 1994), and none are significantly different from the grand mean (8.6% ± 5.2%).

Discussion

P. clavata has a measurable top-down role in both wet and moist tropical forests. Despite the fact that foragers most frequently collect nectar, the ant is clearly adapted to preying on arthropods in two distinct forests and can efficiently kill a wide variety of lepidopteran larvae. The potential effect of *P. clavata* on plant biomass seems large. The ant's appetite for *Atta* alone, which are dominant herbivores in the neotropics (Hölldobler & Wilson, 1990), provides measurable protection for trees (as alluded by Wetterer, 1994). Given the prevalence of predatory ants in tropical forests (Floren *et al.*, 2002), it is likely that *P. clavata* nest trees were occupied by other predatory ants, and my own unquantified observations at La Selva and BCI support this assumption. Thus, the protection afforded by *P. clavata* is probably enhanced by other species of ants, and a comparison of trees with presence versus absence of a normal complement of predatory ants would likely yield an even larger difference in herbivory.

The prey consumption reported here is less than the consumption values documented in 9 other studies of tropical and temperate insectivores (Shelly, 1986; rates range from 4.6 – 107.8 dry-weight g d^{-1} ha^{-1}), but these studies included multiple species (1-56) of predators per hectare. One other forest study that examined prey consumption rates by tropical ants (Franks & Bryant, 1987)

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reported that the dry weight insect consumption of the army ant, *Eciton burchelli* Westwood, was 1.7 g d^{-1} ha^{-1} at BCI. This value is only slightly smaller than that calculated for *P. clavata* at BCI (if wet-weights are converted to dry-weights). If the ants are viewed as a non-dominant part of an ant or predator mosaic (Majer, 1976; Davidson, 1998), and if the other predators have consumption rates that are similar to *P. clavata*, then top-down control is certainly a major component of community dynamics in these systems. However, there are far too few studies that actually quantify natural levels of predation in unmanipulated ecosystems, thus it is difficult to compare rates of predation (or the role of top-down forces) in tropical versus temperate forests (Dyer & Coley, 2001), or even to categorize the predation rates of *P. clavata* as high, medium or low.

It is surprising how little variation was exhibited between colonies at BCI versus La Selva. BCI is drier with a more pronounced dry season. As total annual rainfall increases and the length of the dry season decreases, tropical forests generally have higher plant diversity (Gentry, 1988), greater primary productivity and stem turnover (Philips *et al.*, 1994), and less seasonal production of new foliage, flowers and fruit (van Schaik *et al.*, 1993). The only ant foraging difference was that colonies at La Selva, the wetter forest, brought back more prey plus nectar. The greater amount of prey consumed at La Selva versus BCI could be part of a general trend where predation is greater in wetter forests, which would help explain patterns of lower herbivory and caterpillar biomass in wetter forests (Dyer & Coley, 2001; Coley & Barone, 1996; J. Barone unpublished data). Within-forest variation, between seasons and colonies, was also low. At both forests, the ant appears to be primarily a nectarivore, but arthropods (and to a smaller extent, various other animal tissues) are a consistent and abundant part of its foraging intake. With the approach utilized here (using different species of prey), it is not possible to distinguish between the hypotheses that lepidopteran larvae at La Selva are better defended or that the ants are choosier in their prey selection. The routine manner in which *P. clavata* foragers attacked and subdued lepidopteran larvae is very similar to the predatory behavior of other ants (Schatz *et al.*, 1997, 2001; Dejean *et al*. 1999a, 1999b; Richard *et al.*, 2001; Djieto-Lordon *et al*., 2001a, 2001b) and strengthens the assumption that the prey items returned to the nest are not necessarily scavenged.

There also appeared to be a high level of nestmate cooperation (including spread-eagling; Richard *et al*., 2001; Dejean *et al*., 2001) during prey capturing, subduing, and returning to the nest. This cooperation, in conjunction with the graded recruitment and discriminable trails exhibited by *P. clavata* (Breed *et al.*, 1987), allows these ants to be very effective predators, enabling them, for example, to prey on larvae more than 10 times the mass of an individual ant. While large prey size is generally thought to be an important deterrent to predation by invertebrates (Montllor & Bernays, 1993; Pyke, 1984), the recruiting and cooperating strategies of *P. clavata* allow them to effectively increase their size as predators so that they are less sensitive to the size of their prey (Dyer, 1995).

The significance of ants as predators with respect to their positive effects on plant biomass via killing herbivores such as lepidopteran larvae and leafcutting ants has been examined extensively in myrmecophytes (e.g., Janzen, 1966; Beattie, 1985; Jolivet, 1996; Vasconcelos and Casimiro, 1997; Letourneau, 1998), but it is clear that the predatory role of ants is important beyond these specialized systems (e.g., Dejean *et al.*, 1992; Floren *et al.*, 2002). Basic observational approaches, such as simple quantifications of predation rates, are a necessary part of understanding the community-level effects of predatory ants. Many excellent studies of ant predation have utilized artificial experimental approaches, such as offering prey items to ants (e.g., Dyer, 1995; Richard *et al.*, 2001; Floren *et al.*, 2002), but predation rates measured in these experiments are not necessarily correlated to natural predation rates and cannot easily be compared to other species of ants or to ants from other forests. As demonstrated by the current study, ants may readily consume experimentally offered prey, but that does not signify that they are primarily predaceous, nor does it equate to high predation rates if the offered prey items are different (e.g., have different defenses, see Dyer 1995) from the most abundant prey items. Simple parameters such as average predation rates of abundant predators, such as those reported here and in other natural (Finnegan, 1974) or applied systems (Ibarra-Nunez et al., 2001) are useful parameters that can allow for meaningful comparisons between natural and managed ecosystems.

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