in the type of webs placed on shrubs and trees. This could be the result of a structural constraint that limits the ability of spiders to build three dimensional webs on shrubs. However, we observed both types of webs on each substrate, but proportionally more orb webs on shrubs. Additionally, webs tended to be oriented more vertically on shrubs than trees. That web type and angle of placement differ between placement sites suggests that different prey capture strategies may be more effective in different locations. Substrate clearly affects the form and orientation of spider webs, and further studies of building patterns could lead to a better understanding of the effects of site selection and orientation on damage and prey capture efficiency of spider webs.

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Circadian foraging patterns in *Paraponera clavata*

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Abstract: Paraponera clavata is a large ponerine ant that feeds on nectar and insects in the understory of tropical forests. Although foraging activity of this ant has been shown to be higher at night than during the day, the mechanism behind this increased rate is unclear. I predicted that individual workers would forage both day and night, becoming more active after dark, and that insect abundance and activity would he higher at night, resulting in a larger percentage of insects in the food brought back to the nest. While I found no difference in the percent composition of food by day versus night, it appears from observations of individually marked ants that daytime workers do remain active and increase their foraging rate at night, but are also joined by a group of exclusively nocturnal foragers.

Key Words: ant foraging, food availability, giant tropical ant, nectar, social organization

Introduction

The giant tropical ant, *Paraponera clavata*, is a common understory forager in the Atlantic coastal lowlands of Costa Rica whose nests are constructed at the bases of large trees and house colonies of 700 to 1,400 workers. This species has been observed to be most active at night, although some workers can be found on foliage and tree trunks during daylight hours (Janzen and Carroll 1983). It is not known, however, whether this nocturnal increase in activity is the result of a general increase in foraging rate, or whether there is some division of labor among workers between day and night, with a larger "night shift" taking over once the sun goes down. Be-

cause these eusocial yet relatively primitive ants are solitary foragers that do not recruit colony members to food sources or exhibit organized colony defense (Wilson 1971, Janzen and Caroll 1983), I hypothesized that *P. clavata* would not exhibit the colony-level organization required to finely divide foraging effort. I thus predicted that the same workers observed during the day would forage at night as well, but at a higher rate.

Novello (1999) observed that *P. clavata* most commonly returned to the nest with drops of nectar or nothing at all, although the ants feed on insects as well. He also found, however, that they did not show a preference for one type of food over the other, and suggested that they are opportunistic foragers, simply taking the first item they find. I predicted, due to my preliminary observations of increased nighttime insect abundance, that the percentage of insect food brought back by ants would be greater at night than during the day assuming that insect activity would be greater at night.

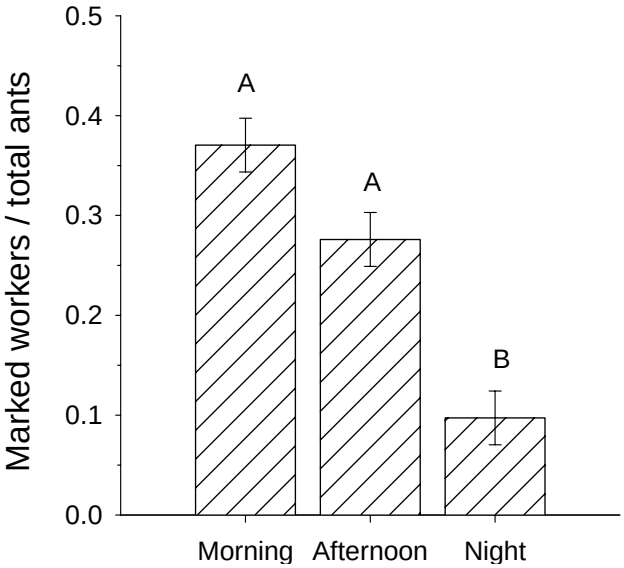

Figure 1. Ratio of marked individuals to total workers in the morning, afternoon, and at night. ($F = 25.63$, $df = 1, 18$, $P < 0.0001$). Letters distinguish means within columns that are significantly different (Tukey comparison $\alpha = 0.05$).

METHODS

On 13 February 2005, I marked 70 *P. clavata* worker ants in a colony beside the Arboretum Trail, approximately 30 m from the laboratory at La Selva Biological Research Station, Costa Rica. These haphazardly selected individuals were captured using forceps and marked with a white paint pen. I then performed six sets of four 0.5-h observations: two in the morning (0700 - 0900, 0900 - 1100), two in the afternoon (1300 - 1500, 1500 - 1700), and two in the evening (2200 - 2400, 2400 - 0200). For each observation period, I recorded the number of marked individuals, workers carrying nectar, workers carrying insects, and total ants entering and leaving the nest. For night observations, I used the low-intensity beam of a headlamp to illuminate the tree in order to view the ants with minimal disturbance.

I compared total ants observed, number and percentage of marked individuals, and percent nectar and insects between day and night using 2-way ANOVAs, fitting a full model testing for effects of time of day, and sampling date. Analyses were performed using JMP 5.0.1, and data conformed to the assumptions of parametric tests.

Table 1. Mean numbers of total ants, marked ants, and ants returning with nectar or insect food in the morning, afternoon, and at night. Letters distinguish means within columns that are significantly different (Tukey comparison $\alpha = 0.05$).

	Total Ants	Marked Ants	Percent Ants with Insects
Morning	a 12.6 ± 6.2	a 5.9 ± 1.4	a 38.5 ± 8.3
Afternoon	a 29.9 ± 6.2	a 7.6 ± 1.4	a 42.8 ± 8.3
Night	b 185.6 ± 6.2	b 17.4 ± 1.4	a 28.5 ± 8.3

RESULTS

The total number of ants observed differed as a function of both time of day ($F = 236.02$, $df = 2, 18$, $P < 0.0001$) and sampling date ($F = 28.03$, $df = 1, 18$, $P < 0.0001$). More ants were observed at night than during the morning or afternoon (Table 1), and more were observed on the second sampling date (95.0 ± 5.1 SE) than the first (57.1 ± 5.1 SE; $F = 7.58$, $df = 5, 18$, $P < 0.004$). There was no interaction between time of day and sampling date ($F = 1.10$, $df = 2, 18$, $P = 0.38$).

The abundance of marked individuals varied only with time of day ($F = 680.25$, $df = 2, 18$, $P < 0.001$) There were more marked individuals entering or leaving the nest during the night than during the morning or afternoon (Table 1). There was no difference between sampling dates ($F = 60.17$, $df = 1, 18$, $P = 0.07$), nor was there an interaction between time of day and sampling date ($F = 31.58$, $df = 2, 18$, $P = 0.38$).

The ratio of marked individuals to total workers observed was significantly lower at night, but there was no difference between numbers observed in morning and the afternoon (Fig. 1). There was no difference between sampling dates ($F = 2.19$, $df = 1, 18$, $P = 0.16$), and no significant interaction between date and time of day ($F = 2.19$, $df = 2, 18$, $P = 0.15$).

The percent of insects (ants carrying insects/total ants returning with all food types) in the ants' diet did not vary as a function of time of day ($F = 0.78$, $df = 2, 18$, $P = 0.47$). There was no difference between sampling dates ($F = 0.16$, $df = 1, 18$, $P = 0.70$), and no significant interaction between date and time of day ($F = 0.07$, $df = 2, 18$, $P = 0.93$).

DISCUSSION

As I predicted, the number of marked individuals entering and leaving the nest increased from day to night, suggesting that workers active during the day increase their foraging rate once night falls. The percentage of total ants made up by marked individuals decreased, however, indicating that unmarked workers not active during the day came out to forage at night. It is possible that these "night shift" ants, having spent the day resting, could forage at a higher rate, entering and leaving the nest more often than workers that are active at all hours. This would amplify the observed difference in percentages of marked individuals. No difference was found in percentage of marked individuals between morning and afternoon observations, suggesting that this influx of new

foragers takes place entirely after sundown instead of gradually over the course of the day.

Contrary to my predictions, there was no change in relative composition of the food brought back by foraging workers as the day progressed. It is possible that, while insects are generally more active at night, there is no change in the abundance of the slow or dead insects that are most easily encountered and subdued by foraging ants (Janzen and Connell 1983). Droplets of transparent nectar were difficult to see in the daylight but reflected the light of my headlamp at night, and at least part of the observed increase in nectar retrieval may have been due to better nighttime visibility. This would artificially increase the daytime insect percentage and might conceal a real difference between day and night.

While patterns in one *P. clavata* colony may not hold true for the species as a whole, it is interesting nonetheless that these ants, whose social organization seems at first glance to be relatively primitive compared to more eusocial species, exhibit a division of labor in foraging that is so seemingly complex. These results suggest that further investigation into the specific roles of workers within the colony and how those roles are determined could reveal an unexpected degree of sophistication in these giants of the ant world.

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