Food preference and foraging behaviors of the giant tropical ant, *Paraponera clavata*

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Abstract: Giant tropical ants, *Paraponera clavata*, are frequently observed carrying insects and nectar to their nests. However, very little is known about their foraging preferences and strategies. I predicted ants would carry nectar to their nest most frequently because it would be the food type most frequently encountered in nature, but when given a choice, *P. clavata* would prefer to forage on insect prey because of the higher energy content. I found significantly more nectar being taken to the nest, but found no difference in prey chosen when both were equally available. Finally, I observed *P. clavata* capturing live prey, proving that they are capable of predatory behavior. It appears that *P. clavata* is an opportunistic forager, feeding upon whatever food type is first encountered.

Key Words: bala ants, food choice

INTRODUCTION

The giant tropical ant, *Paraponera clavata* is among the most remarkable ant species of the tropics. Measuring 22 mm in length it is the largest ant species in Central America, can be extremely aggressive to intruders, and has a sting which is considered among the most painful of all insects (Janzen and Carroll 1983). Colonies of several thousand individuals occur at the base of trees, where most workers travel up the trunk into the canopy to forage, eventually returning to the nest carrying insect parts or nectar in their mandibles. When they discover a large food source, they may lay a pheromone trail for others to follow by dragging their gasters (specialized structures on the abdomen) on the way back to the nest (Breed and Bennett 1985).

Despite the conspicuousness of *P. clavata*, few studies have considered its fundamental biology, particularly feeding habits. There have been several reports linking food type, abundance, and distance from nest to recruitment levels (e.g. Breed et al. 1996b; Breed et al. 1997), but I found no reports about the proportion of each food type *P. clavata* carries to their nests. Hubbard (1995) attempted to determine food preferences for these ants in captivity, but was unsuccessful because of high ant mortality.

I predicted that proportionately more ants would carry nectar back to the nest than insect prey, as nectar is likely more readily and dependably available in the canopy than other food types. I further predicted that *P. clavata* would prefer to feed upon insect prey rather than nectar, because insects offer a greater energetic benefit than nectar (Fewell et al. 1996). Support for a possible preference for insect prey is given by Breed et al. (1987) who found that more workers were recruited to insect prey than a nectar source.

When foraging, specific workers do not specialize on a particular food type (Breed et al. 1987), yet I found no conclusive study of Janzen and Carroll's (1983) question of whether *P. clavata* scavenges or hunts insect prey. I tested whether *P. clavata* would hunt and kill live invertebrates during their foraging, having little intuition or information to make a prediction.

METHODS

Sampling took place on 16-18 February 1999 at La Selva Biological Research Station, Costa Rica. All sampling took place between 22:00 and 05:00, when *P. clavata* is most active (Janzen and Carroll 1983; Shrot 1991). My sample sites consisted of two nests located in primary forest, and four in the arboretum, which has a clear understory but a complete canopy. Ant activities in the arboretum are similar to those in primary forest (Breed et al. 1996a), so I combined data from the two habitats. Nests were chosen haphazardly by searching for *P. clavata* on trees.

Before making any experimental manipulations to the colony, I recorded the number of ants returning to each nest with food items over a 10 min period. I refer to this as the "natural foraging" observations.

Next I designed an experiment to test whether *P. clavata* prefers nectar or insects. I made an artificial "nectar," using a 20% sugar solution as outlined by Breed et al. (1996b). I used dead katydids (Orthoptera, subfamily Tettigoniidae) as insect prey, as suggested by Breed et al. (1997). At each tree, I then took the caps from three soda bottles and placed a strip of tape on the back. Each cap was pinned (through the tape) to the main foraging trail on the trunk of the tree, oriented vertically 1-2 m from the ground. I cut a katydid into small pieces, making each piece approximately the same size as several drops of nectar. The small size of this insect material presented to *P. clavata* was also chosen to create a low probability of recruitment to the prey, so as not to alter the encounter probabilities or behaviors at the other experimental "stations" (Breed et al. 1997). I then pinned a small piece of katydid adjacent to each of the three bottle caps. Finally I placed three drops of nectar solution in each bottle cap, a volume small enough that there would be little recruitment to the site (Breed et al. 1997). I recorded which food type was chosen by the first ant to make a food selection at each of the three "stations," whether this food type was the first encountered, and made notes about the feeding behaviors observed.

To test whether *P. clavata* is a predator, I placed a total of seven caterpillars on the foraging trails of several colonies. This was intented to simulate natural encounters of prey by the ants.

RESULTS

In the 10 min natural foraging observations, there was a significant difference in prey items returned to the nests. The number (mean ± 1 SE) of ants carrying nectar back to the nest was 40.7 ± 5.9, while only 15.2 ± 2.4 ants were carrying insects back to the nest. This higher proportion of ants carrying nectar was found at all six colonies, and the difference in the proportions of nectar:insect foods was highly significant (paired t-test: $t = -25.83$, $df = 5$, $P < 0.0001$; Fig. 1).

There was no difference in food preference by *P. clavata* in my experiments. In the food preference trials ($n = 18$), 10 ants chose insects, while eight chose nectar (Likelihood Ratio: $X^2 = 0.22$, $df = 1$, $P = 0.64$). Although my sample size was small for a broad behavioral categorization, there was almost no variation of foraging behavior between any of the six nests. In 16 of the 18 trials the ant chose to eat the first food type encountered. In the other two cases, one ant foraged on the nectar, the other on the insect. There was no pattern of food choice within individual colonies, no colony had the same food type selected in all three trials.

When caterpillars were placed upon the foraging trail, the ants did not seem to notice their presence until physical contact was made. Upon contact, the ant would quickly attack, grabbing the insect in its jaw and attacking it with their stinging abdominal probe. Pieces of the prey were then taken by several ants, and carried to the nest. Of the seven caterpillars placed on the foraging trail, three were successfully killed, indicating that *P. clavata* is not limited to scavenging behaviors.

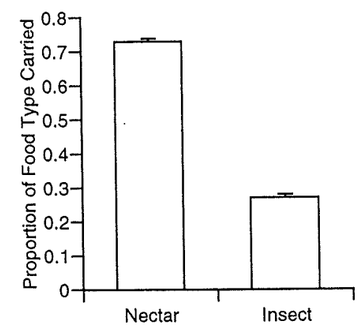

Fig. 1. Proportion of two basic food types brought back to the nest by *P. clavata* ants during 10 min trials from six different nests (mean ± 1 SE) ($p < 0.0001$).

DISCUSSION

As predicted, I observed significantly more ants carrying nectar back to their nest than any other food item. However, my results also indicate that the ants do not forage based on a preference for nectar, as they almost always chose the first food type encountered. Observations indicated that they could sense

only what their bodies - particularly their antennae - touched, as they would frequently pass within several cm of the food displays without diverting their course. Perhaps the high proportion of ants returning to the nest with nectar was due to ants finding nectar sources in the canopy more frequently than they encountered insect prey.

I also observed that the proportion of ants carrying each food type was not consistent over short time periods within the 10 min natural foraging observations. I would frequently observe a "run" of several ants carrying insect parts to the nest, followed shortly by several ants carrying nectar. In the experimental food preference trial, I observed up to eight ants aggregating around a single food source, although they were not recruited by the foraging ant laying down a pheromone trail. It is possible that *P. clavata* searches for the first food type encountered and then alerts other colony members to the location of the food, so the food can be partitioned and transported to the nest.

I did not observe any aggressive behavior among ants within the aggregations around the food source. By using their antennae, newly arriving ants would communicate with ants around the food resource, and the feeding ant would move so that both could forage at the same time. When space did not permit all ants to forage simultaneously, the extra ants would wait for the other ants to finish eating before working their way to the food resource. This behavior is contrary to the aggressive interactions seen among many predatory and scavenging animals, and may be due to the eusocial nature of these ants.

That *P. clavata* attacked and killed the caterpillar prey indicates that it is not simply scavenging for dead insects, but is capable of killing them when encountered. The success rate of *P. clavata* encountering and killing prey was low (less than 50 %), perhaps due to poorly developed hunting senses such as vision.

The results of this study indicate that although certain food types may be more beneficial to *P. clavata* energetically, their sensory input is limited to whatever food items they encounter. *P. clavata* therefore forages on whatever is first encountered, regardless of the proximity of a potentially more beneficial food type.

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