BULLET PROOF: ECOLOGICAL STOICHIOMETRY AND THE DIURNAL FORGING PREFERENCES OF BULLET ANTS (*PARAPONERA CLAVATA*)

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Abstract: Optimal foraging in colonies may be related to the relative requirements for different nutritional resources (e.g., nectar vs. protein). I studied bullet ants, *Paraponera clavata*, in La Selva Biological Reserve, Costa Rica. Based on a model of optimal foraging, I hypothesized that ants would preferentially recruit to nectar by day and to protein at night. I also hypothesized that ants would forage preferentially for either nectar or protein. Ants showed a clear preference for nectar over protein, regardless of distance from nest. There was no diurnal pattern to their preferences or activity. It remains unclear the extent to which bullet ants forage flexibly to match their resource acquisition to their nutritional requirements.

Keywords optimal foraging, ant behavior, La Selva

INTRODUCTION

Optimal foraging behavior is dictated by the abundance and distribution of food resources as well as by the relative requirements for various resources at any given time. Frequently, organisms must forage for various food items to satisfy their nutritional needs.

Ants, for example, could forage opportunistically, such that they consume or recruit to whatever they stumble upon. Alternatively, ants may forage or recruit preferentially to the resource that is typically most limiting for them. Finally, ant foraging and recruitment behavior could be finely tuned to the nutritional stoichiometry of the colony, such that they forage preferentially for the resources that are currently most limiting (e.g., energy or protein), even though that may change from day to day, week to week, or season to season. In either of the latter two cases, foragers should tend to invest more energy and time for a food item that is of a greater value to them. Ants forage for both sugars, in the form of nectar and homopteran exudates (honeydew), and for protein. They need both to survive, but the relative value of each should vary based on which substance is more limiting to colony growth and reproduction.

Bullet ants (*Paraponera clavata*) are common in the La Selva forest. *P. clavata* is a common understory forager in the Atlantic coastal lowlands of Costa Rica. Its nests are constructed at the bases of large trees and house colonies of 700 to 1,400 workers (Janzen and Carroll 1983). It is a predator-scavenger and collects

protein, plant parts, and water droplets (Young & Hermann 1980). Extra-floral nectar is also a principal dietary component (Hermann 1975, Breed & Bennett 1985, Fewell et al. 1992). The ants take droplets of water and nectar back to their nests to feed other adults or to feed larvae. Larvae are also fed with various arthropods, other invertebrates, and occasionally pieces of small vertebrates (Young & Hermann 1980, Morgan 1996). Preliminary daytime observations suggested that ant preference of nectar or protein varied by time of day.

I created and tested two theoretical models based on these facts. The first model predicts that ants would recruit equally to sugar or protein, possibly in relation to how far they need to go to get it. While the second model predicts that one resource should have higher value to the ants and that they should recruit preferentially to one or the other, and/or be willing to go further to get it.

I hypothesized that these ants would adjust their foraging methods diurnally due to competing availability for nectar and protein. I also hypothesized that ants would forage optimally based on nectar and/or protein available. Specifically, I predicted that ants will forage more for protein at night, due to increased amount of arthropods and invertebrates as well as a decrease in amount of nectar production in flowers and plants. I also predicted that foraging will be increased at night, as reported by Raffensperger (2005) and supporting the prediction that ants adjust there foraging methods due to competing needs. An alternate model is that ant foraging behavior is canalized such that they opportunistically collect whatever food resource they stumble upon first.

METHODS

On 18 - 20 February, 2008, I opportunistically sampled *Paraponera Clavata* colonies in the Arborium, a 3-ha area of secondary forest ca. 1 km southeast of Estación Biologia La Selva, Costa Rica. I tested for preferential responses of ants to alternative food resources at five times each day. Ants were offered a choice of one 5 mL dispenser of artificial nectar (5-6 g) (Table 1) and another with 2 cm^2 of protein in the form of raw fish (8-14 g). All tendons and striation were removed from the fish for ease of carrying and collecting by the ants. A third vial with 5 mL of nectar was used as a control for nectar evaporation rate at each time interval.

Each vial was weighed with nectar or protein inside of them before and after a 1-hour encounter with the ant colony. The two vials were placed in random directions between 0.25 - 2 m away from the ant nest within a 180° arc on the

northwest side of the tree. I recorded the amount of time to discovery and number of ants recruited for each of the vials in the field. Ants labeled as "recruited" were those that stayed at the nectary for more than 5 seconds and/or collected provisions. After 1 hour, I recorded the weight of consumed nectar or protein in the lab using the Ohaus Scout digital scale. Prior to statistical analysis, a square root transformation was applied to the number of ants recruited and the time to discovery.

Table 1. Ingredients of artificial nectar. From Cincinnati Zoo Insectarium & Botanical Garden *P. clavata* exibit.

Artificial Nectar Ingredients
300 ml Distilled water
4 rounded tbsp. (50-60 g) Table sugar (sucrose)
Electrodex Electrolyte mix and Thorne Reseach Basic Nutrients III Multivitamin (about 0.05 g each)

RESULTS

I was able to record ant foraging behavior for a total of 10 observation hours. The number of ants recruited to food resources declined with increasing distance from the nest (F = 4.02, df = 3,16, P = 0.026; Fig. 1), but there was no interaction between resource type and distance from nest. There was no significant difference between the time to discovery by distance from nest (ANOVA, F = 0.60 df = 3,16, P = 0.63; Fig. 2). Ants recruited more strongly to nectar than protein irrespective of time of day or distance from the nest (ANOVA, F = 7.08, df = 1,18, P = 0.0159). Also, the per capita amount of food resource consumed for nectar was higher than that of protein (t = 5.51, df = 9, P = 0.0002; Fig 3). There was no apparent diurnal pattern in the number of ants recruited (Fig. 4).

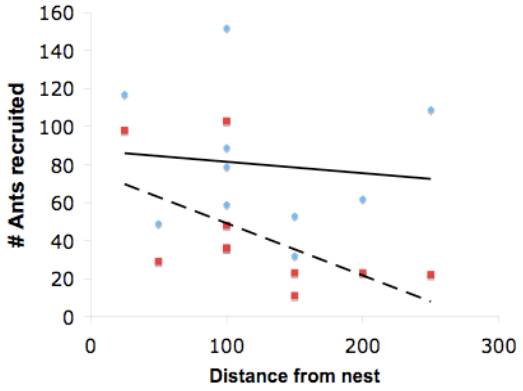

Figure 1: Number of ants recruited to each food resource vs. distance from nest for bullet ants in La Selva, Costa Rica (diamonds = nectar,, squares = protein). Each line is a best fit of data points for protein and nectar, solid line is for nectar and dashed line is for protein.

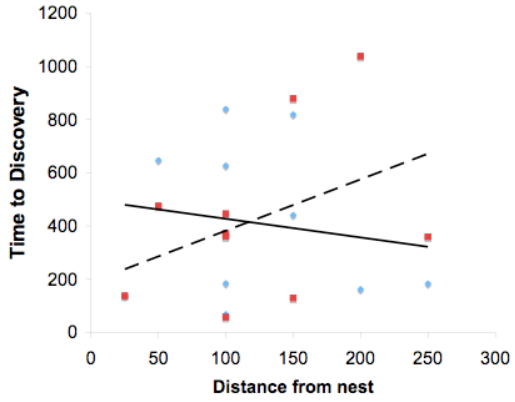

Figure 2: Time of discovery (seconds) vs. distance from nest (meters) for bullet ants in La Selva, Costa Rica.(diamonds = nectar, squares = protein). Each line is a best fit of data points for protein and nectar, solid line is for nectar and dashed line is for protein.

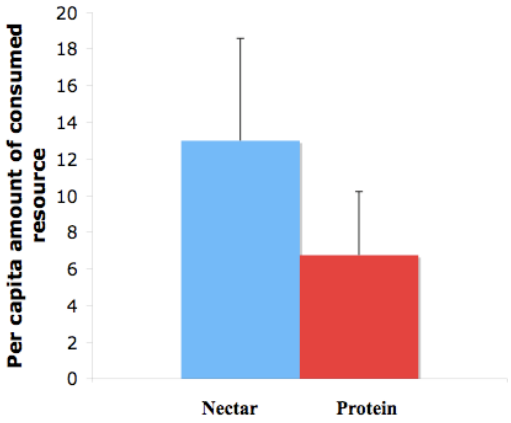

Figure 3: Per capita amount of consumed resource (mg / ant). Error bars are ±1SE, back-transformed to original units.

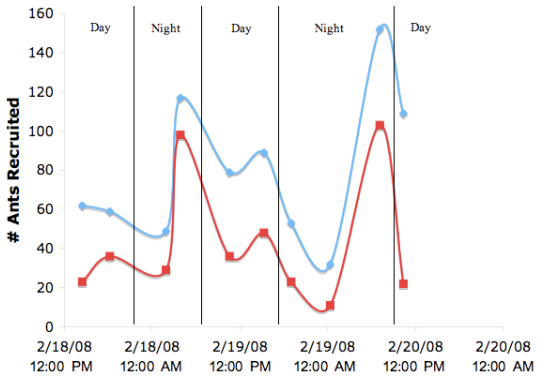

Figure 4: Number of ants recruited to each food source vs. time of day/night for 18-20 Feb. Diamonds (top line) represent data points for nectar, squares (bottom line) represent data points for protein.

DISCUSSION

Bullet ants showed a clear and striking preference for recruiting foragers to nectar over protein. This could reflect the fact that they are limited more by nectar so they will invest more in the searching for and collecting of nectar. It remains unknown whether ants search more actively for nectar, but the colony collected it more vigorously when they found it. It is still uncertain whether the preference for nectar is optimal because we have no independent evidence whether the ants are more limited by sugar or protein.

It could be informative to test ant preferences for sugar vs. protein when they do and do not have larval brood to feed. If there is seasonality to their breeding, their must be seasonality to their stoichiometric requirements (more protein requirements when larvae are growing).

It was surprising that there was no effect of distance from nest on the time to discovery because the area to search increases more than linearly with distance from the nest. This could have been an artifact of small sample sizes (the ants got lucky and found my nectar quickly), but it also suggests the possibility that the ants are using olfactory senses to locate nectar – perhaps with greater efficacy than they would locate distant prey.

Larger sample sizes with similar designs would help clarify the patterns, but my results included 10 hours of experimental observations, so the basic patterns should be reasonably robust.

I sampled a different ant colony on 19 February at 1353 and was surprised to see that these ants were actively collecting moss from the tree bark, almost ignoring my

nectar and protein dispensers. This could mean that the ants of this colony had a brood because plant pieces are reportedly used to frame spinning larvae, for pupal bedding and to line nest chamber walls (Morgan 2006).

Ants did not seem to forage more at night than during the day, contrary to the observations of Raffensperger (2005) at the same site. It remains unknown how the relative availability of resources, and potential predators, varies between day and night.

Further insights into the ecological stoichiometry of bullet ants could be gained from studies that include colonies in a range of habitats, sample across seasons, over a longer time period, or across different climatic patterns. Such studies could ascertain whether these ants are optimally foraging for the needs of the colony and/or individual, vs. the alternative that their movements and preferences are relatively autonomous and inflexible.

Figure 5: Close-up of *Paraponera clavata* outside nest. 19 Feb 2008. Photo by Alex Spinoso.

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