

LEAF-CUTTER ANTS (*ATTA CEPHALOTES*) ARE SIMILARLY ABUNDANT IN PRIMARY AND SECONDARY FOREST

STEPHEN J. TAERUM

Faculty editor: Matthew P. Ayres

Abstract: Forest disturbances strongly influence herbivore-forest interactions. I examined how forest disturbances affect the abundance of leaf-cutter ants, *Atta cephalotes*, at La Selva Biological Reserve in Costa Rica. In addition, I tested for evidence of different plant palatabilities between primary and secondary forests, and tested for differences in interspecific interactions involving *At. cephalotes* in both forest types. Contrary to previous studies, leaf-cutter ant abundance tended to be higher in primary forests than secondary forests. There was no difference in feeding preferences of *At. cephalotes* on leaf pieces collected from the two forest types. In addition, there were more minimas hitchhiking on leaves carried by foragers in primary forest, suggesting that parasitic phorid flies may be more abundant in primary than secondary forest. Future studies should elucidate the causes of these patterns.

Key words: disturbance, herbivory, interspecific interactions, tropical forests, leaf-cutter ants

INTRODUCTION

Forest disturbance can affect herbivore populations by changing plant species compositions, and by altering community interactions between herbivores and their natural enemies, competitors, and mutualists. In turn, herbivores influence forest structure and function by speeding or slowing successional processes, increasing or decreasing plant diversity, and altering trophic interactions. The effects of forest disturbance on herbivores, and the reciprocal impacts of herbivores on disturbed forests, are of great interest in tropical forests, where human activities are converting large amounts of primary forest to secondary forest.

Depending on the circumstances, forest disturbance could harm herbivore populations (for example, by removing obligate food sources) or benefit them (for example, by lowering the abundance of natural enemies). Leaf-cutter ants, *Atta cephalotes* (Formicidae: Attini), often have higher densities in secondary forests than in primary forests suggesting that *At. cephalotes* benefit from certain disturbances (Farji-Brener 2001). *At. cephalotes* feed on a mutualist fungal cultivar that the ants provision with leaves, fruits, and flowers from a diversity of plants. This symbiosis makes *At. cephalotes* a generalist herbivore that may more readily adjust to changes in plant community than specialist herbivores. In addition, the fungal

cultivar is negatively affected by plant secondary compounds, which are more prevalent in climax tree species (which dominate primary forests) than pioneer species (which dominate secondary forests). Therefore, higher palatability of plants may result in higher *At. cephalotes* densities in secondary forests than primary forests.

At. cephalotes may also benefit from low abundances of natural enemies or competitors in secondary forests. Enemies of *At. cephalotes* include phorid flies that attack foraging ant workers, and the specialist fungal parasite, *Escovopsis*, which attacks leaf-cutter ant fungal cultivars. Populations of *At. cephalotes* could be favored by forest disturbance if secondary forests are unfavorable for these or other enemies. In addition, *At. cephalotes* competes for resources with other herbivores, such as other leaf-cutter ant species. Low competitor abundances in secondary forests would tend to increase *At. cephalotes* abundance.

Alternatively, *At. cephalotes* abundance may depend on soil properties that are correlated with forest disturbance more than they are influenced by primary vs. secondary forest directly. For example, human development (and therefore forest disturbance) tends to be concentrated on areas with good soils and plants growing on high nutrient soils tend to produce less

anti-herbivore defenses such as tannins. So *At. cephalotes* could be more abundant in areas of high nutrient soils, which tend to be the areas where forest disturbance by humans is most likely. Soil type could also influence *At. cephalotes* if some soils are more suitable for nest excavation.

The purpose of this study was to determine which of the above theoretical models explain the abundance patterns of *At. cephalotes*. I estimated ant abundances in both primary and secondary tropical forests to determine if *At. cephalotes* has a higher abundance in secondary forests, and I sampled primary and secondary forests on both alluvial (i.e., nutrient-rich) and residual (i.e., nutrient-poor) soils to separate the contributions of soil type *At. cephalotes* abundance (Nichols-Orians 1991). I collected data at 3 separate times of day to test if the foraging habits of *At. cephalotes* remain constant throughout the day, or if foraging increases during daytime, as previously shown with *At. colombica* (Liebert and Ruel 1994).

I conducted assays to test if *At. cephalotes* preferentially select leaves from secondary forest over leaves from primary forests, as predicted if leaf palatability is higher in secondary forests. I tested indirectly for habitat differences in parasitic phorid flies (Diptera: Phoridae) by comparing the proportion of foraging workers (medias and

maximas) that carried minima workers on their leaf fragments (minor workers are hypothesized to protect foraging workers from phorids). Finally, I examined the abundance of *At. colombica* near the *At. cephalotes* nests to test if competitors are more or less abundant in different forest types.

METHODS

During 18 – 20 February 2008, I studied the abundance of *At. cephalotes* in the La Selva Biological Reserve in Costa Rica. La Selva was ideal for this study as it has large areas of primary and secondary forest on both alluvial and residual soils.

I conducted field observations on the evening of the 18th (starting at 21:00), the afternoon of the 19th (starting at 13:00), and the morning of the 20th (starting at 08:00). I established four 20 × 200 m transects along concrete or dirt trails within 2 km of the La Selva Biological Station such that one transect was on each of the following forest type-soil combinations: primary forest on alluvial soil (Camino Experimental Sur trail), primary forest on residual soil (Sendero Surá trail), secondary forest on alluvial soil (Sendero Tres Rios trail), and secondary forest on residual soil (Lindero Occidental trail). I started the transects at random distances from the starts of each trail.

During my initial observation period, I walked the length of each transect and counted the trails of *At. cephalotes* and *At. colombica* (which compete with *At. cephalotes* for resources) within each transect. I followed each leaf-cutter ant trail carefully to prevent counting a leaf-cutter ant trail more than once. For all observation periods at each *At. cephalotes* trail, I counted the number of ants that crossed an imaginary line within 2 minutes. To calculate *At. cephalotes* abundances, I obtained the mean values of the ants counted in 2 minutes for each transect, and multiplied these means by the number of trails observed in each transect. If ants carried leaves during the observation period, I sampled 20 leaf-carrying workers and counted the number of those leaf fragments that had minor workers.

On 18 February, I collected 40 leaf pieces each from *At. cephalotes* workers foraging in the primary and secondary forests (no more than 15 pieces from any one trail). On the afternoon of 19 February, I placed a line of 20 leaves on one active *At. cephalotes* trail on each transect, alternating leaves collected in the primary and secondary forests. I counted the leaf pieces that remained from the primary and secondary forests the following morning to test for preference between leaves from both forest types.

RESULTS

I observed a total of nine *At. cephalotes* trails on my transects: six in the primary forest (three on alluvial soil, three on residual soil) and three in the secondary forest (one on alluvial soil, two on residual soil). No *At. colombica* trails were observed on any transects. I counted a total of 1181 *At. cephalotes* workers across all observation periods. Although some ants foraged throughout the day, diurnal foraging seemed to be minor. I only observed 12 ants during the afternoon and 5 ants at morning, as opposed to 1164 ants at night. Consequently, I excluded the afternoon and morning data from analyses.

At. cephalotes were not more abundant in secondary forests. Actually, they tended to be more abundant in primary than in secondary forests (Figure 1a), although the difference was not significant ($t = 2.52$, d.f. = 2, $P = 0.13$). There was no apparent difference in *At. cephalotes* abundance between forests on alluvial vs. residual soils (Figure 1b; $t = 0.01$, d.f. = 2, $P = 0.99$). Minor workers on leaves were more common on *At. cephalotes* trails in primary than in secondary forests ($t = 2.32$, d.f. = 7, $P = 0.053$; Figure 2). *At. cephalotes* workers showed no preference for leaf pieces collected in primary or secondary forest ($t = 1.46$, d.f. = 3, $P = 0.12$; Figure 3).

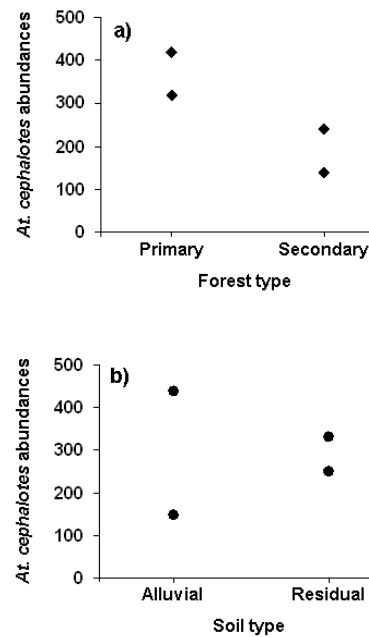


Figure 1. *At. cephalotes* abundances a) in primary vs. secondary forests and b) on alluvial vs. residual soils.

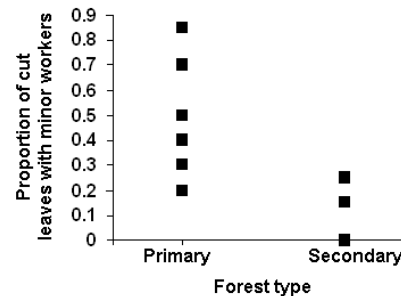


Figure 2. Proportions of *At. cephalotes* workers that carried minor workers on their leaves in primary and secondary forests.

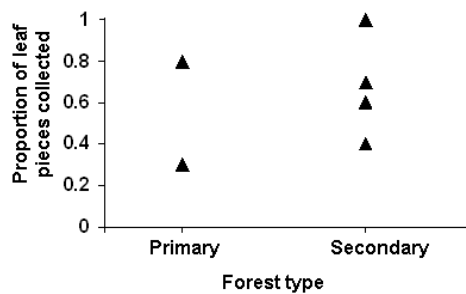


Figure 3. Proportions of leaf pieces originating from the primary and secondary forest that were collected by *At. cephalotes* workers in the preference assays.

DISCUSSION

My studies failed to support previous findings that *At. cephalotes* is more prevalent in secondary forest than in primary forest. Perhaps different mechanisms influence patterns of leaf-cutter ant abundance at La Selva than at other locations. Higher *At. cephalotes* abundances in primary forests than in secondary forests may suggest that *At. cephalotes* are adapted to the plants in primary forests, that secondary forests are less suitable for nest or trail construction than primary forests (e.g., because of high tree density), or that secondary forests favor an enemy of *At. cephalotes* or its mutualist fungus. Of course it is also possible that more intensive sampling would reveal a different pattern. Low sample sizes in my study would have increased the likelihood of spurious patterns (e.g., from chance location of transects relative to nests of *At. cephalotes*).

Future studies could conduct more thorough tests of spatial patterns in ant abundance.

There seemed to be a striking difference in forest types in that there was a higher frequency of minor workers travelling with foraging workers in primary than secondary forest. This suggests that more phorid parasitism may be more intense in the primary forest. This was the opposite of my theoretical prediction, as *At. cephalotes* abundances were higher in the primary forest than the secondary forest. However, these patterns might be explained if phorid prevalence depends on *At. cephalotes* abundances, or if phorids are more able to find or track leaf-cutter ants in primary forests. Additional studies that quantify phorid prevalence as well as studies examining the interactions between minor workers and phorids are required. In addition, future studies could evaluate the prevalence of other parasites on *At. cephalotes*, such as mites or *Escovopsis*, in primary and secondary tropical forests.

At. cephalotes showed no preference for leaf pieces from primary or secondary forest, suggesting that leaves from both forest types were equally palatable. This argues against the importance of the resource availability hypothesis of genotypic patterns in plant defenses for explaining patterns in *At. cephalotes* abundance.

However, the sample sizes were again quite small, and results may have been biased because ants in the primary forest likely preferentially foraged on the most palatable plant species in the primary forest. Therefore, the leaf pieces collected in both forest types may have been equally palatable, even if primary forests have fewer palatable plant species. Alternatively, the trails in the primary forests may have led to more palatable trees in secondary forests.

Although the soil properties I examined did not affect *At. cephalotes* numbers, other soil properties, such as grain size and moisture retention, may influence *At. cephalotes* abundance. Future studies could address how these additional soil properties influence leaf-cutter ant abundance.

Nowogrodzki, A.R., R.W. Trierweiler, and S.A. Hunter. 2005. The hickhacker's guide to the leaf-cutter colony. Dartmouth College, Hanover, NH. Pp. 98-101.

LITERATURE CITED

- Farji-Brener, A.G. 2001. Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. *Oikos* 92: 169-177.
- Liebert, A.E., and J.J. Ruel. 1994. Diurnal and temperature related patterns in *Atta cephalotes* trail use. Dartmouth College, Hanover, NH. Pp. 62-65.
- Nichols-Orians, C.M. 1991. Environmentally induced differences in plant traits: Consequences for susceptibility to a leaf-cutter ant. *Ecology* 72: 1609-1623.

MULTIPLE NAVIGATION STRATEGIES IN THE BULLET ANT *PARAPONERA CLAVATA*

BRIAN M. LAPPAS, ALANNA H. PURDY, DYLAN D. THOMAS,
THOMAS J. LOBBEN, AND ROBERT H. YANKER III

Faculty editor: Matthew P. Ayres

Abstract: Hymenoptera foraging efficiency is contingent upon the collective ability of workers to locate resource patches and then navigate between the patches and the nest. Ant species are known to vary in the extent to which they rely on pheromone and visual cues for orientation. Bullet ants are a neotropical species that lack caste differentiation and are thought to have relatively primitive abilities to employ pheromone foraging trails. On the other hand, these attributes might be adaptive because they are generalist foragers. Although bullet ants were sometimes slow to discover a new resource patch, they showed a rapid learning curve in navigating back and forth from the nest to the patch, and were surprisingly efficient in recruiting new foragers to the recently discovered patch. Manipulations of the trail substrate indicated that the ants were able to opportunistically develop and exploit a pheromone trail, but did not use the pheromone trail to the exclusion of other cues. Bullet ants thus have versatile navigation abilities that probably enhance their ability to harvest small diffuse patches of resources in tropical ecosystems.

Keywords: ant navigation, learning, pheromones, recruitment, travel time

INTRODUCTION

Two important features of ants which contribute to their ecological success are the ability to orient while foraging, and the ability to develop specialized castes which perform different functions. However there is considerable variation in these features among ant species, with some species using different orientation strategies and completely lacking castes. Some species, such as *Iridomyrmex humilis*, have evolved sophisticated pheromone systems that permit efficient foraging by large numbers of workers to and from distant

concentrated food sources (Aron et al. 1992). A potential disadvantage is that these species are often totally reliant upon pheromones, and are unable to find the trail if lost or removed from it. Other ants, such as *Lasius niger*, rely less on chemical cues and can find their way back to the nest when a pheromone trail has been removed (Aron et al. 1992).

The bullet ant, *Paraponera clavata*, lacks differentiated castes and is thought to resemble the primitive condition of ants with only partial use of pheromones in foraging (Choe and Crespi 1997). These features might constrain their ecological success relative to more

derived ant species with well developed castes and highly evolved pheromone systems, and explain their relatively small colony size and total biomass. Alternatively, it might be that these attributes of *P. clavata* make them well suited to their pattern of resource use. Morphological specialization of castes limits the foraging versatility of individuals, thus a homogenous morphology might be optimal for generalist foragers. They do not form large foraging columns, and forage primarily on small diffuse food sources such as insects and nectar sources close to the nest, which could render pheromone trails less cost-effective. It has even been shown that *P. clavata* makes use of other orientation cues such as canopy contrast, and nonpheromonal environmental odors (Ehmer 1999). Thus, rather than being evolutionarily constrained, their homogenous morphotype and reduced pheromone dependency may be optimal for their particular ecological niche.

We tested how well the bullet ants use pheromone trails, and if they are able to orient themselves using other means. We predicted that bullet ants would use the pheromone trail when available, and that recruitment would increase with pheromone strength, but also that the ants would be able to orient themselves after the removal of their

pheromone trail via other environmental cues.

METHODS

We studied the behavior of two colonies of *P. clavata* on two separate trees in the arboreum (ca. 500m and 510m on the path SUR) of La Selva Biological Station, Costa Rica on 20-21 February 2008. We created artificial nectaries using a solution of 4 tablespoons sugar, a pack of Electrodeux Electrolyte mix, and one Thorne Research Basic Nutrients III Multivitamin (about 0.05 gr.) in 300 mL water, and set up dishes filled with this solution approximately 1 m from each nest. We began recording data when the first ant found the nectar.

Our first treatment monitored the dynamics of recruitment to a food source. We kept a running count of the total number of ant that had left the nectary to return to the nest (referred to as ant #). To track the apparent learning curve of individual ants, we marked the first ant with a white pen, and tracked its time going from the nectary to the nest (referred to as travel time) for its first seven trips. As more ants were recruited to the nectary, we recorded the travel times of randomly selected ants, indexed by ant # (e.g.: ant #, travel time).

Once a strong pheromone trail appeared to be established (indicated by stable travel times), we

began our second treatment. In this manipulation we blocked their established pheromone trails placing a bag covered in fresh soil gathered nearby over them. We continued counting ant # and travel times to assess their response.

Once the travel times back to the nest were stable again, we implemented our third treatment, a preference test for the ants at the nectary. To do this, we rotated the pheromone trail so that it led away from the nest (Figure 1).

We counted the number of ants at the nectary before Treatment 3, and compared the number of ants which followed the old trail (pheromone) with the number of ants which appeared to be taking other paths and presumably using other forms of navigation (e.g., visual memory, terrain usage, magnetic orientation). We ended the experiment when all of the ants that were at the dish left (to guard against effects of establishment of a new pheromone trail).

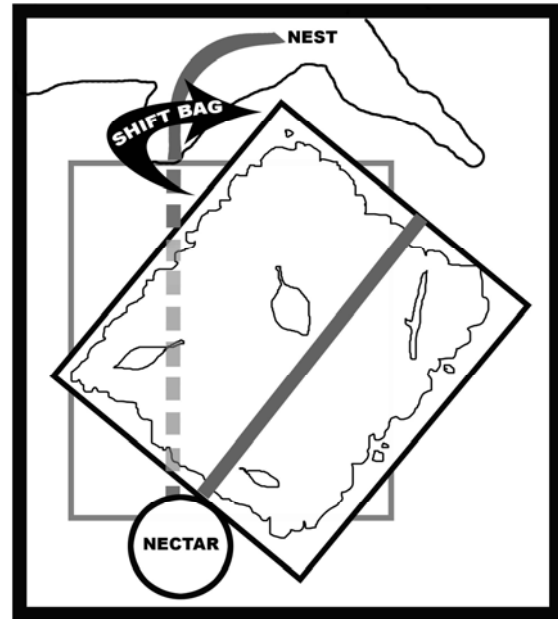


FIGURE 1. Experimental setup for manipulations of bullet ants in the arboreum of La Selva, Costa Rica. The gray rectangle represents a garbage bag covered in dirt which we placed over the path of ants going from the nectar to the nest. After a new pheromone trail had been established over the garbage bag, we rotated it away from the nest and assessed the proportion of ants following the pheromone trail (gray line) versus going straight back to the nest (dashed line).

RESULTS

In all experiments, the first trip back to the nest required the longest time, and subsequent return times decreased non-linearly until reaching a minimum by an individual's 3rd or 4th trip to the nectar (Figure 2). Apparently, individual ants became increasingly proficient at retuning to the nest, due to the pheromone trail becoming stronger, improved use of other cues, or both. Travel duration of all foragers was quickly minimized

once a strong pheromone trail was established to the nectar (Figure 3).

After removing the pheromone trail with a plastic bag, the ants became disoriented and stridulated frequently. However, the ants cautiously established a new pheromone trail over the dirt on the bag, and back to the nest. Right after this treatment, trip duration first increased dramatically, and then quickly decreased to pre-treatment times after ca. 10 foragers had re-established the route. In two of the four experiments, the average trip time after the treatment was longer than the average trip time before it was applied, which was likely due to more difficult terrain (sticks, leaves) laying over the initial pheromone trail. We inferred from the slope of the curve in Figure 5 that there was roughly the same number of foragers before and after the experimental manipulation.

To assess the importance of pheromones for navigation, we presented the ants with conflicting pheromone and visual cues by creating a pheromone trail that pointed away from their intended destination. Before the rotation of the bag, 100% of the ants followed the putative pheromone trail upon leaving the nectar dish. After the rotation, the ants did not randomly disperse from the nectary, for all of the ants either headed either along the new direction indicated by the pheromone trail, or in the correct

direction towards the nest. Contrary to expected if bullet ants were completely reliant on pheromones, a significant fraction of the ants at the nectary went in the correct direction, and did not follow the pheromone trail. In the first tree, only 15 out of the 27 ants at the dish followed the pheromone trail. Thus, the direction in which ants headed upon leaving the nectary after the treatment was significantly different compared to before the treatment (Fisher's exact test, $p < 0.0001$). In the second tree, only 1 of the 6 ants took the pheromone trail, and the remaining 5 headed straight to the nest; this also significantly different than before the treatment (Fisher's exact test, $p < 0.0001$).

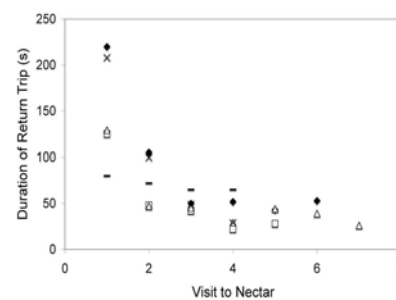


FIGURE 2. Relationship between the return trip duration of the first ant to find the nectary and its number of visits to it at La Selva, Costa Rica. Symbols differentiate first foragers from six separate experiments.

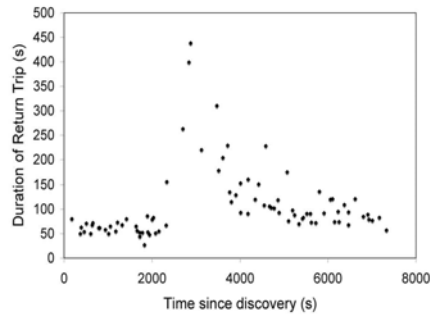


FIGURE 3. Duration of return trips versus total time since first discovery of nectar of bullet ants in La Selva, Costa Rica. The spike in trip time corresponds to an experimental treatment in which we covered their pheromone trail.

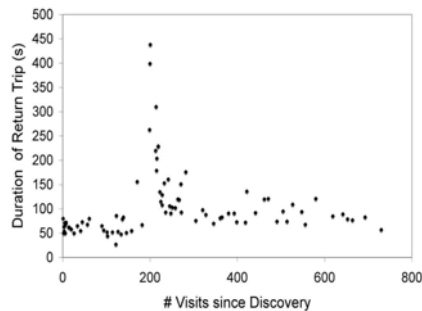


FIGURE 4: Duration of return trips versus the total number of visits to that nectar source by bullet ants in La Selva, Costa Rica. The sudden increase in duration after 200 visits corresponds to an experimental treatment in which we covered their pheromone trail.

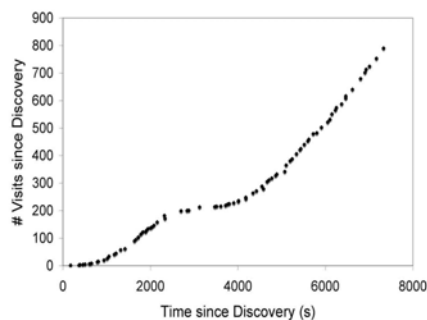


FIGURE 5. Cumulative number of visits to a Petri dish filled with nectar versus time since initial discovery of it for bullet ants in La Selva, Costa Rica. The plateau corresponds to an experimental treatment in which we covered their pheromone trail.

DISCUSSION

Our results argued against the hypothesis that bullet ants are intrinsically poor foragers that lack the orientation abilities of more derived ant groups. Instead, bullet ants can apparently use a flexible combination of pheromones and environmental cues to orient themselves. Although they were sometimes slow to find the artificial nectary (it usually took 15-120 minutes for an ant to discover it), after the first ant returned to the nest, its learning curve was surprisingly fast (Figure 2). Recruitment was also faster than might be expected for ants that are minimally eusocial (Figure 5). Within a few minutes of discovering the resource patch, all of the potential foragers were engaged in harvesting the nectary, and were moving as quickly as the terrain permitted. Our data suggests that as more ants walk to and from the nectary, pheromone strength increases, and consequently trip time decreases to a minimum determined by the distance and terrain (Figure 4).

The choice experiment was particularly telling by showing that the ants do not necessarily blindly follow the pheromone trail, as tends to be the case for leaf-cutter or army ants. This implies that bullet ants can use means other than pheromones to

navigate. Having multiple navigation strategies could be an adaptation to small colony size and diffuse resources. If local resources tend to be limited, the colony would benefit more from individualistic foraging of ants, which enhance the chances of locating additional resource patches. Presumably the cost : benefit ratio of establishing a pheromone trail to a local resource patch increases when fewer ants are going to employ the trail before it is depleted. The result that at least as many ants returned to the nectary after the first disturbance suggests that the reward was great enough that it was worthwhile for the ants to invest considerable effort to re-establish the connection between the nest and the nectary.

It is not known exactly how ants navigate in the absence of pheromones. The simplest possibility is that they resort to visual cues, but other possibilities include scents (volatile pheromones or nonpheromonal), spatial memory, or even magnetic fields (Banks and Srygley 2003). We hypothesize that vision is important, but it is not obvious what visual cues are being exploited.

LITERATURE CITED

- Aron, S., R. Beckers, J.L. Deneubourg and J.M. Pasteels. 1993. Memory and chemical communication in the orientation of two mass-recruiting ant species. *Insectes Sociaux* 40:369-280.
- Banks, A.N., and R.B. Srygley. 2003. Orientation by magnetic fields in leaf-cutter ants, *Atta colombica* (Hymenoptera: Formicidae). *Ethology* 109:835-846.
- Choe J.C., and B.J. Crespi. 1997. Morphologically 'primitive' ants: comparative view of social characters, and the importance of queen-worker dimorphism. Pages 372-391 in Choe J.C., editor. *The evolution of social behavior in insects and arachnids*. Cambridge University Press, Cambridge.
- Ehmer, B. 1999. Orientation in the Ant *Paraponera clavata*. *Journal of Insect Behavior* 12: 711-722.
- Aron, S., R. Beckers, J.L. Deneubourg and J.M. Pasteels. 1993. Memory and chemical communication in the orientation of two mass-recruiting

RELATION OF CALLING QUALITY IN MALE *DENDROBATES PUMILIO* TO TERRITORY QUALITY

LIA M. CHEEK

Faculty editor: Matthew P. Ayres

Abstract: Vocalizations are frequently costly but can increase fitness through defense of mates and territory. The ability of organisms to adequately defend or establish these territories may depend on their ability to vocalize. I tested relationships between calling and territory quality in *Dendrobates pumilio*. The hypothesis was that males who called for longer periods of time and with higher frequency would hold better territories. In fact, leaf litter depth on the territory was positively correlated with the 2nd axis of a principal components analysis of calling patterns. Results also indicated a negative correlation between calling quality and the duration of second calls. Litter depth might affect territory quality by providing oviposition sites, by providing habitat for ants on which the frogs prey; or it might be correlated with something else that is directly important to the frogs. In any case, leaf litter depth is linked to frog calling, and may be linked to frog fitness as well.

KEYWORDS: Strawberry poison dart frogs, frog vocalization, La Selva Costa Rica

INTRODUCTION

Vocalizations are important for communication in many organisms, e.g., to protect resources and attract mates. Vocalization is energetically costly, and variation in strength and quality of vocalization can be due to variation in the resources an individual has access too, or to their body size. It may also be due to variation in abiotic factors such as rainfall, soil moisture or types which may create less or more optimal conditions for calling.

Dendrobates pumilio, the Strawberry Poison Dart Frog, is a classic example of this use for vocalization. *D. pumilio* males use vocalization to attract females with

which to mate and to protect their territory from other males. *D. pumilio* females are attracted to males who can call with the most endurance (Heike, 2003), which suggests there may be a correlation between calling quality (as defined by endurance and frequency) and territory quality. Some variables contributing to territory quality for male *D. pumilio* may be the amount of leaf litter (which can provide oviposition sites and perhaps habitat for their ant prey), and the amount of bromeliads that can provide phytotelmata for tadpoles. Presence of adequate perches for males to call from (0-2 m from ground) as well as the presence of a food source (small ants and termites) may also be important

factors of territory quality. I hypothesized that males with high quality territories would need to call more vigorously to adequately defend their territory than males with low quality territory. This was inseparable from the related idea that males who can call better will be able to establish and hold better territories. Alternatively, males with poor territories may have higher quality calls to remain sexually competitive with males in high quality territories. Finally, there may be no relationship between calling quality and territory quality, and the establishment of territory may depend more upon physical displays and interactions (Janzen 1983) than on calling quality.

METHODS

I collected data from 0800 on February 18th to 1100 on February 20th 2008 in Heredia, Costa Rica. I marked and collected data from 13 territories along Sendero Tres Rios (0 - 600m), Sendero Sura (0 - 350m) and within the Arboleda at La Selva. After I identified male *Dendrobates pumilio* by their calls, I located and marked male *D. pumilio* positions and territories (estimated as a circle with a 4m radius around the frogs' locations). I then evaluated Male *D. pumilio* calls by measuring call length, the resting time between calls, and the frequency of calls (amount of individual chirps per 10

seconds). I took these measurements over two days from 0600-1100 to control for the diurnal patterns in frog calls. I evaluated male territory quality by counting calling perches (logs or horizontal structures 0 - 2m off of the ground), the number of bromeliads, leaf litter depth at 3 points within the territory, and the abundance of ants within the territory (evaluated with pitfall and sticky traps). I analyzed the data by running a Principle Components Analysis on the variables that make up call quality (call duration, frequency, and proportion of time calling, for 1st and 2nd calls). I then evaluated alternative models to predict call quality (1st two axes of PCA) based upon independent measurements of territory quality.

RESULTS

The number of small ants and termites captured by my sticky traps and pitfall traps was negligible in all sites; so I had to omit direct measures of food abundance from my analyses. There was no relationship between any measures of habitat quality and the 1st PCA axis of frog calling ($F < 2.5$, $df = 4, 7$, $P > 0.13$). However, the 2nd PCA axis of frog calling was significantly positively related to leaf litter depth (Fig. 1, $r^2 = 0.61$, $F = 5.79$, $df = 1, 7$, $P = .047$). The factor loadings for PCA-2 for duration of calls 1 and 2, frequency of calls 1 and 2, and

proportion of time spent calling, were 0.685, -0.489, -0.264, 0.471 and 0.0173, respectively.

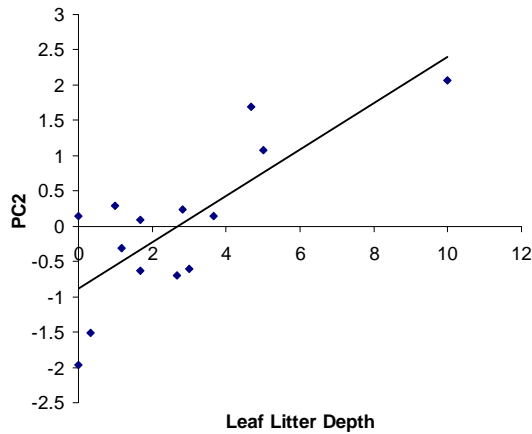


Figure 1: Regression of leaf litter depth vs PCA2 (descriptor of calling quality of male *Dendrobates pumilio*, Data from La Selva Research Station, Heredia, Costa Rica. r^2 value = .61

DISCUSSION

Results partially supported the hypothesis that territory quality (Fig. 1) positively related to calling quality. This could either be because males who call better can hold better territories, or that males who hold better territories must call more to defend their desirable territories. Further study on *D. pumilio* would be required to separate these possibilities.

My interpretations are based on the assumption that leaf litter depth is related to territory quality. I support this assumption based on two possible mechanisms. The litter

may be important for oviposition sites (Janzen, 1983). Also, leaf litter depth can be related to the abundance of arthropods (Lieberman, 1982), especially ants, which are the primary food resource of *D. pumilio*. Food provides energy for mating and, in the case of *D. pumilio*, calling for mates. Chow et al. (2005) found correlations between leaf litter depth and the abundance of *D. pumilio* supporting my assumption of the importance of leaf litter in territory quality. Conte et al. (2000), who also studied territoriality in *D. pumilio*, suggest that reproductive resources do not influence territory selection of male poison dart frogs. However, their measurement of bromeliads related to the reproductive resources used by females, while the process of oviposition, directed by males (Janzen, 1983), is related to the leaf litter in an area.

The positive correlation between PC2 (calling quality) and duration of call suggests that duration of call 1 is an important factor of calling quality. This is consistent with reports that selection of males by females is largely based upon call endurance (Heike, 2003). The negative correlation between PC2 and the duration of call 2 may reflect the energetic expense of calling (better callers use more energy on the first call and have less to devote to their second call, shortening its duration).

Vocalization by Strawberry Poison-Dart frogs, like that of many other territorial species, is apparently related to the quality of territories that they hold, and is presumably a partial determinant of their fitness.

LITERATURE CITED

- Chow, E. C., S.A. Hunter, J.E. Jun, and E.L. Sharp. 2005. Effect of food resources on the abundance of *Dendrobates pumilio*. Dartmouth Studies in Tropical Ecology 2005, pp. 118-122.
- Conte, M. N., L. E. Aucoin, B.C. Shannon, and S. E. LaPlante. 2000. Factores determining territoriality in the Strawberry Poison-Dart frog, *Dendrobates Pumilio*. Dartmouth Studies in Tropical Ecology 2000, pp. 116-120.
- Janzen, D.H. 1983. Costa Rican Natural History. The University of Chicago Press, pp. 398-399.
- Heike P. 2003. Variation in male calling behavior and relation to male mating success in the strawberry poison-dart frog (*dendrobates pumilio*) Ethology 109: 273-290.
- Lieberman, S.S., C.F. Dock. 1982. Analysis of leaf litter arthropod fauna of a lowland tropical evergreen forest site (La Selva, Costa Rica). Revista de Biologia Tropical 30: 27-34.

A DANGER IN DENSITY: THE EFFECTS OF HOST DISTRIBUTION ON LEAF EPIPHYTE ABUNDANCE

IAN G. WHEAT

Faculty editor: Matthew P. Ayres

Abstract: Natural enemies of plants can influence plant distribution and abundance. Epiphylls are generally regarded as structural parasites of plants, a kind of natural enemy. I studied epiphylls of *Geonoma cuneata* to test if the local density of this understory palm affects the density of epiphylls as plant density can affect herbivore density. This extension of the Janzen-Connell model predicted that aggregated plants would have a greater epiphyll density. Epiphyll density was higher in aggregations of *G. cuneata*, which could produce a feedback in which plant density affects epiphylls, which in turn affects plant density.

Key Words: phyllosphere, foliicolous epiphytes, fishtail palm

INTRODUCTION

One reason cited for the apparent imperative of wide dispersal in plants is to escape natural enemies. The theory is that if seeds are dispersed close to the parent tree, herbivores, parasites and other natural enemies of that species of plant will more easily locate or spread to the vulnerable young plants, preying on them, reducing their chance to survive and grow, and reducing their fitness. This force is especially strong in tropical rainforests, and has been invoked as a reason why the local diversity of tropical trees is so high (Queensborough et al. 2007). It follows that if plant natural enemies are important, the risks for adult plants, as well as seedlings, may be higher when the plants occur in high density.

The phyllosphere is of broad importance because most of terrestrial photosynthesis occurs on the surface of leaves. In tropical forests with high moisture, foliicolous epiphytes are conspicuously abundant on the surface of lichens. While the knowledge of their ecology is limited, the leaf surface they occupy has clear detrimental effects on the host plant (Pinokiyo et al. 2006). I studied the fungal, lichen and bryophyte epiphylls of *Geonoma cuneata*, a common understory palm, at the La Selva biological preserve in Costa Rica. I compared epiphyll density on *G. cuneata* leaves of plants in high and low density patches, as well as plants within both types of patches with and without immediate neighbor plants of the same.

I hypothesized that high density would facilitate the spread of

epiphylls that can grow on *G. cuneata* from one plant to another, and that density at the scale of the local patch would be more important in the spread of foliicolous epiphytes than the presence of immediate neighbors. From these hypotheses, I predicted that I would find greater epiphyll density for plants in dense patches than for isolated plants and that I would find little or no difference in epiphyll density between plants with and without immediate conspecific neighbors.

METHODS

On the 18 – 20 February 2008, I collected leaf samples from the Camino Circular Cercano and Camino Experimental Sur trails of the La Selva biological preserve, Costa Rica. I walked a random number of strides (1 – 60) on the trail, and five meters off the trail to opportunistically look for two *Geonoma cuneata* plants to measure. I sampled plants in high density stands, defined as fifteen or more other *G. cuneata* within a five meter radius, and plants in low density areas, defined as less than four plants within a five meter radius. For each plant I recorded if it had any neighboring *G. cuneata* within a one-meter radius.

For each plant I measured stem length and ranked available light on a scale from one to five. I measured epiphyte density on a

random leaf of each sample plant, with the restriction that it be on the fourth growth ring to control for leaf age. On each leaf, I ran two 25-cm transects, measuring at each cm the presence or absence of fungus, lichen or bryophytes. I added these values together to estimate total epiphyte density for the leaf. I applied a square root transformation to normalize the data for statistical analysis.

RESULTS

There was a greater density of total epiphytes on the leaves of plants in dense patches than in isolated patches ($t = 8.56$, $df = 46$, $p < 0.0001$). of the same pattern applied for all three epiphyte taxa: fungus ($t = 3.86$, $df = 46$, $p = 0.0004$), lichen ($t = 7.30$, $df = 46$, $p < 0.0001$) and moss (Kruskal-Wallis $S = 690$, $df = 22$, $p = 0.0058$).

There was no significant difference in total epiphyll density in isolated patches between plants that had close neighbors vs. those that did not ($t = 0.14$, $df = 22$, $p = 0.89$), nor was there any significant difference for fungus, lichen or moss density. In dense patches there was greater epiphyll density for plant with close neighbors ($t = 2.72$, $df = 22$, $p = 0.0125$). This difference was largely driven by a greater lichen density for plants with close neighbors ($t = 4.19$, $df = 22$, $p = 0.0004$). Fungal abundance varied in

the same direction ($t = 1.74$, $df = 22$, $p = 0.096$), and moss density did not vary (Kruskal-Wallis $S = 162.5$, $df = 22$, $p = 0.44$).

There was no change in total epiphyll density with height of plant stem ($r^2 = 0.01$, $df = 1,46$, $p = 0.57$). There was a nearly significant trend of decreasing total epiphyll density with increased sunlight ($r^2 = 0.07$, $df = 1,46$, $p = 0.08$). This trend was driven by a decrease in lichen density with increased light intensity ($r^2 = 0.10$, $df = 1,46$, $p = 0.0001$). There was no significant change in fungus density ($r^2 = 0.00$, $df = 1,46$, $p = 0.77$), or moss density ($r^2 = 0.00$, $df = 1,46$, $p = 0.64$) with light intensity.

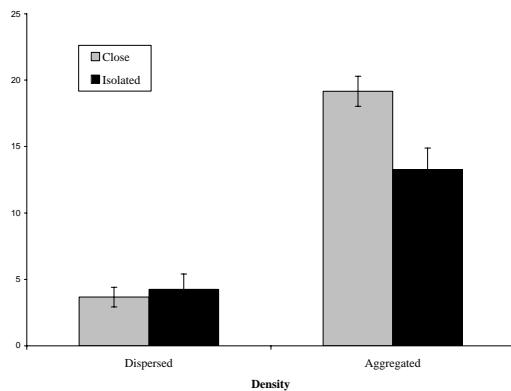


Figure 1. Estimated epiphyll density by *G. cuneata* density at five-meter (dispersed vs aggregated) and one-meter radius (close vs. isolated).

DISCUSSION

The number of *Geonoma cuneata* within a five-meter radius was related to the abundance of epiphylls. Presumably foliicolous epiphytes can disperse from plant to

plant more easily when their host is aggregated. This explanation requires that epiphylls be in some part dispersal limited, which seems likely since the surface of the leaf is never fully covered. The greater epiphyll density for plants with close neighbors in aggregations may reflect that higher *G. cuneata* density at the scale of one-meter radius intensifies the effects created by the five-meter scale aggregation, further facilitating the spread of epiphylls from plant to plant. Notably, local abundance did not produce the same effect. Apparently density at the five-meter scale is more important in the spread of epiphylls. This might be a clue about the mode and tempo by which epiphyll propagules move from plant to plant.

Because epiphyll density did not change with stem length, I inferred that variation in plant size (presumably related to age) did not influence the effect of host plant aggregation on epiphyte density. Similarly, light had little effect, except for lichens, which were negatively related to light, perhaps due to the effects of desiccation or heat stress.

Fungal, lichen and bryophyte densities all increased similarly with aggregation, suggesting similarities in their ecology. Moss was only found on leaves of aggregated plants, and of these relatively few. Yet moss tended to occur at high density when present on a leaf. This

may indicate that relative to the other epiphylls they are competitively dominant and especially dispersal limited. Lichens were the most abundant epiphylls in *G. cuneata* and showed the greatest response to changes in density. Fungus was affected to a lesser degree by changes in host density, and this may be due to its higher density on dispersed and isolated host plants. Follicolous fungi may be better dispersers than lichens or bryophytes.

One problem with the application of the natural enemies theory is that it is unclear if epiphytes are truly structural parasites, or in fact commensalists. The epiphytic cover of many *G. cuneata* leaves was enough that it seems probable that they reduce photosynthesis, and these understory plants are probably generally light limited. While epiphylls are often thought of as having a parasitic relationship with their host plant, other research has pointed to possible benefits of epiphylls for host plants, complicating the relationship. There is some evidence that follicolous epiphytes may reduce leaf herbivory or provide extra nutrients (from nitrogen fixing lichens) that compensate for, or even outweigh, their detrimental effects (Pinokiyo et al. 2006). It seems clear that plant dispersion influences the epiphylls. If the epiphylls are ecological

antagonists or protagonists of the plants, then the epiphylls may produce a feedback system in which the effect of plant density on epiphylls may in turn determine the distribution of host plants.

LITERATURE CITED

- Pinokiyo, A., K. P. Singh and J. S. Singh.
2006. Leaf-colonizing lichens: their diversity, ecology and future prospects. *Current Science* 90: 509-518.
- Queensborough, S.A., D.F.R.P. Burslem, N.C. Garwood and R. Valencia.
2007. Neighborhood and community interactions determine the spatial patterns of tropical tree seedling survival. *Ecology* 88: 2248-2258.

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

ALEX C. SPINOSO

Faculty editor: Matthew P. Ayres

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 their 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 Biología 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 cm² 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* exhibit.

Artificial Nectar Ingredients
300 ml Distilled water
4 rounded tbsp. (50-60 g) Table sugar (sucrose)
Electrodex Electrolyte mix and Thorne Research 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).

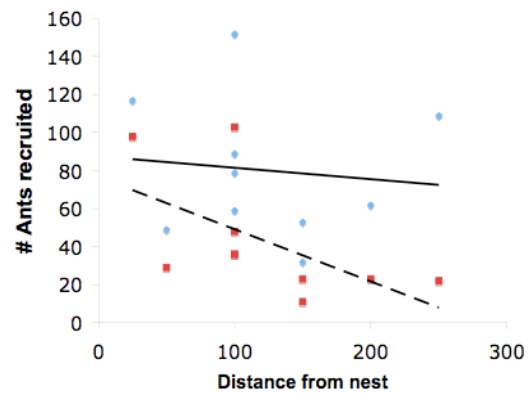


Figure 1: Number of ants recruited to each food resource vs. distance from nest for bullet ants in La Selva, Costa Rica (diamonds = nectar,, squares = protein). Each line is a best fit of data points for protein and nectar, solid line is for nectar and dashed line is for protein.

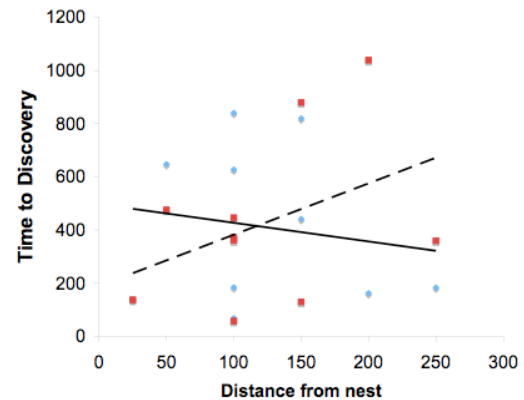


Figure 2: Time of discovery (seconds) vs. distance from nest (meters) for bullet ants in La Selva, Costa Rica.(diamonds = nectar, squares = protein). Each line is a best fit of data points for protein and nectar, solid line is for nectar and dashed line is for protein.

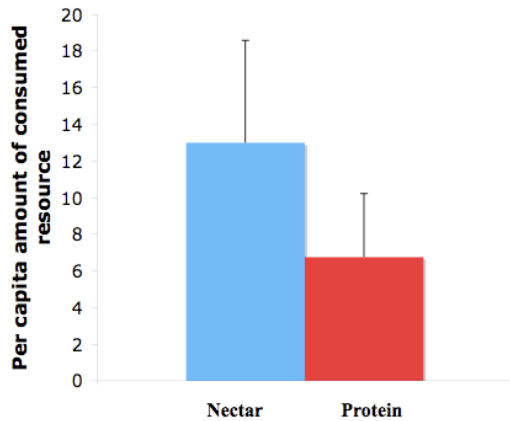


Figure 3: Per capita amount of consumed resource (mg / ant). Error bars are $\pm 1SE$, back-transformed to original units.

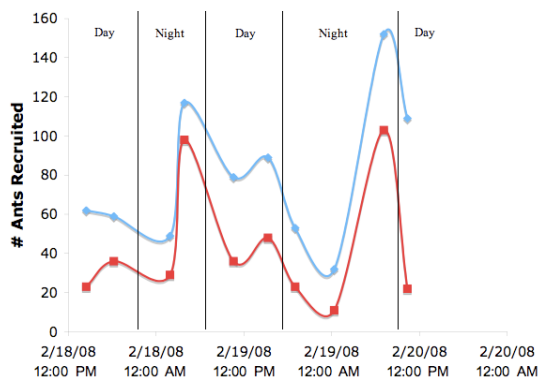


Figure 4: Number of ants recruited to each food source vs. time of day/night for 18-20 Feb. Diamonds (top line) represent data points for nectar, squares (bottom line) represent data points for protein.

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.

LITERATURE CITED

- Breed, M.D. & Bennett, B. (1985): Mass recruitment to nectar sources in *Paraponera clavata* colonies: A field study. *Insectes Sociaux* 32:198-208.
- Fewell, J.H.; Harrison, J.F.; Stiller, T.M. & Breed, M.D. (1992): Distance effects on resource profitability and recruitment in the giant tropical ant, *Paraponera clavata*. *Oecologia (Berl.)* 92:542-547.
- Hermann, H.R. (1975): Crepuscular and nocturnal activities of *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). *Ent. News* 86(5-6):94-98.
- Janzen, D.H., ed. 1983. *Paraponera clavata* in *Costa Rican Natural History*. Chicago, Illinois: University of Chicago Press. p. 394-396.
- Morgan, R.C. (1996): Quest for the giant tropical bullet ant, *Paraponera clavata*. In: 1996 Invertebrates in Captivity Conference Proceedings. Sonoran Arthropod Studies Institute, Tucson, pp. 13-20.
- Raffensperger, J. C. 2005. Diurnal foraging patterns in *Paraponera clavata*.

Dartmouth Studies in Tropical Ecology, 2005. pp. 107-110.

Schmidt, J.O. (1986): Chemistry, pharmacology, and chemical ecology of ant venoms. In: Venoms of the Hymenoptera (Piek, T., ed.). Academic Press, pp. 425-509.

Schmidt, J.O. (1990): Hymenopteran venoms: striving toward the ultimate defense against vertebrates. In: Insect Defenses, Adaptive Mechanisms and Strategies of Protein.

Janzen, D.H. & Carroll, C.R. (1983): *Paraponera clavata* (bala, giant tropical ant). In: Costa Rican Natural History (Janzen, D.H., ed.), Univ. Chicago Press, Chicago, pp.752-753.

Young, A.M. & Hermann, H.R. (1980): Notes on foraging of the giant tropical ant *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). J. Kan. Entomol. Soc. 53:35-55.

TWO CAN PLAY THIS GAME: A STUDY OF TOUCAN DOMINANCE IN THE FRUGIVOROUS BIRD COMMUNITY AT LA SELVA, COSTA RICA

TIFFANY D. CHANG, JENNA M. SULLIVAN, SAMANTHA R. KAPLAN,
ELEANOR B.R. PASCALL, AND YIRAN GU

Faculty editor: Matthew P. Ayres

Abstract: Species co-occurrence in the tropical rainforest could be understood in terms of either equilibrium or non-equilibrium models. Stable equilibrium models postulate that communities are structured, for example by niche partitioning and dominance hierarchies. We proposed that the Chestnut-mandibled Toucan (*Ramphastos swainsonii*) would be behaviorally dominant in the avian frugivore community of La Selva, Costa Rica. We observed 15 interspecific and 8 intraspecific, toucan-initiated aggressive incidents, but there was no statistical support for a dominance hierarchy. However, our study was conducted during the dry season when fruit is relatively abundant. It remains possible that Chestnut-mandibled Toucans actively displace other avian frugivores in the wet season when fruits are limiting. Niche-partitioning was implied by the uneven distribution of non-toucan frugivores. Our study introduces a base-line data set, based on over 29 hours of toucan observation, that may provide a foundation for future toucan research at La Selva.

Keywords: community structure, *Ramphastos swainsonii*, *R. sulfuratus*, *Pteroglossus torquatus*, species coexistence

INTRODUCTION

How so many similar species can co-occur in the tropical rainforest is one of the oldest questions in ecology. The traditional explanation has been that species coexist in a stable equilibrium, which requires some form of community structure. This is typically thought of as niche partitioning, in which species minimize competition through spatial or temporal partitioning of resources. At the other extreme, Hubbell (2001) has proposed a neutral model in which many species co-occur via slow random walks of abundance that inevitably

lead to extinction, but at a rate roughly equal to that of speciation. A related theoretical possibility is that communities can be structured into dominance hierarchies, in which the presence of a dominant species interferes with the natural behavior of others. However, dominance hierarchies raise the question of why the dominant species does not competitively exclude other species to extinction. Thus, dominance is expected to be linked to some other factor that limits the success of the dominant species, such as increased predation or decreased efficiency in locating food sources.

We tested for structure within a guild of the avian community at La

Selva Biological Research Station on the lowland Caribbean slope of Costa Rica. Specifically, we tested for the presence of a dominance hierarchy among avian frugivores, focusing on Chestnut-mandibled Toucans (*Ramphastos swainsonii*), which are reported to displace smaller frugivorous birds in fruiting trees (Janzen 1983; Stiles and Skutch 1989). If the bird community is structured by some form of resource partitioning, we should see a non-random distribution of birds that does not change in the presence or absence of toucans. If instead, toucans are the dominant species in a hierarchy, sub-dominant species will be distributed non-randomly with respect to the presence or absence of Chestnut-mandibled toucans.

METHODS

On 18-20 February 2008, we searched for *R. swainsonii* on the trails of La Selva Biological Station, Costa Rica. Once we found a group of toucans, we visited the site again at a later time to increase the chances of finding them for additional observations.

We conducted opportunistic scans at 3-minute intervals of all visible frugivores in a tree or group of trees (tree stands), noting species, location (top, middle, or bottom of tree canopy), and bird activity (sitting, eating, flying, resting).

Aggressive interactions between birds were noted. Because toucans did not typically aggregate in a single tree, we observed all trees in which toucans were present.

We recorded when birds left tree(s), and stopped observations after all toucans had flown away. We watched the tree(s) for a 10-minute interval immediately afterwards, noting all species' arrivals, their locations, and activities. After these 10 minutes, we returned an hour later and conducted a final 5-minute scan of the site.

Because foraging flocks containing *R. swainsonii* often contained Keel-billed Toucans (*R. sulfuratus*) and Collared Aracaris (*Pteroglossus torquatus*) as well, we grouped *R. swainsonii*, *R. sulfuratus* and *P. torquatus* (toucans) together for our analysis. We assumed that, with similar feeding habits and strategies, these three species of the toucan family (Ramphastidae) would exert a similar effect on other frugivorous birds. We limited our analysis of non-toucan bird species spatial preferences to those species with more than 6 observations.

RESULTS

We found a total of 10 foraging groups containing Chestnut-mandibled Toucans (*R. swainsonii*), Keel-billed Toucans (*R. sulfuratus*), and/or Collared Aracaris (*P. torquatus*). Of all toucan groups

observed, 7 were mixed-species flocks while 2 were of only Chestnut-mandibled Toucans and 1 was of only Collared Aracaris (Table 1). We observed the 10 toucan groups across a total of 26 distinguishable tree stands and found them most often in the early morning (06:00 – 07:00) and late afternoon (15:00 – 17:00), up the station entrance road

to the north and along the forest edge near the Almendro lab. We observed Chestnut-mandibled Toucans for 876 observation-minutes, Collared Aracari for 625 observation-minutes and Keel-billed Toucans for 265 observation-minutes. The total observation time was 29 hrs.

Table 1. Summary of toucan observations with respect to duration, flock composition, and number of aggressive interactions at La Selva Biological Station, Costa Rica. Interspecific aggressive interactions include those with non-toucan birds.

Flock number	Date & Time	Duration in tree stand (min.)	Toucan flock composition (max. number/scan)			# Aggressive interactions	
			Chestnut-mandibled Toucan	Keel-billed Toucan	Collared Aracari	Inter-specific	Conspecific
1	2/18 8:33-8:37	4	5	1	1	3	-
2	2/18 9:05-9:17	12	-	-	10	-	1
3	2/18 15:00-15:27	27	2	-	4	6	-
4	2/18 16:26-17:04	28	1	-	11	3	2
5	2/19 6:29-6:34	5	-	-	3	-	-
6	2/19 6:04-6:15	9	3	-	5	-	-
7	2/19 6:45-6:50	5	-	1	5	-	-
8	2/20 6:01-7:05	64	11	4	-	1	5
9	2/20 6:11-6:16	5	2	-	-	2	-
10	2/20 6:42-6:53	11	3	-	-	-	-
Total		170	27	6	39	15	8

We also observed a total of 16 other frugivorous bird species (non-toucan species), of which we were able to positively identify 6 (Table 2). Montezuma Oropendolas (*Psarocolius montezuma*) were the most common (present in 122 bird scans), implying that they have high local abundance relative to the other 16 species and/or are more likely to use the same resources as toucans.

Table 2. Number of bird scans (154 total) that included each identified bird species La Selva Biological Station, Costa Rica.

Species	Number of bird scans
Montezuma Oropendola (<i>Psarocolius Montezuma</i>)	122
Bananaquit (<i>Coereba flaveola</i>)	15
Red-lored Parrot (<i>Amazona autumnalis</i>)	10
Crested Guan (<i>Penelope purpurascens</i>)	4
Mealy parrot (<i>Amazona farinose</i>)	4
Scarlet-rumped Tanager (<i>Ramphocelus passerinii</i>)	3

Of 6 non-toucan species tested, 5 were unevenly distributed among the top, middle, and bottom of tree canopies. Most birds preferred the middle (406 observations) and top (380) of tree canopy over the bottom (102). This distribution was unaffected by the presence or absence of toucans ($\chi^2 = 0.89$, $df = 2$, $P = 0.005$). Additionally, non-toucan birds were equally likely to be in a tree with or without toucans present ($\chi^2 = 0.02$, $df = 1$, $P = 0.89$). Roughly half (13 of 27) of our observations of non-toucans feeding were in the presence of toucans. However, toucans spent 30% of their time in trees feeding, which was more than twice as often as other birds (Pearson $\chi^2 = 14.16$, $df = 2$, $P = 0.0002$). The three toucan species did not differ in time allocation between behaviors (sitting, flying, resting, eating; Pearson $\chi^2 = 2.50$, $df = 6$, $P = 0.87$).

Although our analyses found no statistical evidence of toucans affecting the presence, distribution or activity of other birds, our

observations did include 15 instances of toucans engaged in interspecific aggressive behavior. Chestnut-mandibled Toucans were the main aggressors, instigating 11 interspecific confrontations in 876 observation-minutes. There were also 8 occurrences of intraspecific aggression: 5 among Chestnut-mandibled Toucans and 3 among Collared Aracaris. Chestnut-mandibled Toucans were also seen in displays of dominance over other toucan species: there were 6 instances of Aracaris displaced by a Chestnut-mandibled Toucan, and 3 instances of Keel-billed Toucan displacement. The most frequent victim of aggression from toucans was the Montezuma Oropendola (4 out of 8 interspecific incidents). On one occasion, we observed a Keel-billed Toucan chase an Oropendola from its branch, only to be chased away moments later by a Chestnut-mandibled Toucan.

DISCUSSION

The spatial distribution of non-toucan birds remained constant regardless of toucan presence and absence, which is inconsistent with the hypothesis that toucans are dominant over other birds. Feeding frequency of frugivores was also unaffected by toucan presence or absence, indicating that toucans do not prevent other birds from foraging. The overall uneven spatial distribution of bird species suggests that all birds prefer similar areas within a tree (potentially because that is where the fruits are), and indicated that toucans do not dominate this community. In other words, two (or more) species can play the "game" of coexistence.

In this tropical rainforest, fruits are more abundant during the dry season than during the wet season. Our study was done during the dry season. It is possible that toucans do not need to exert dominance over other bird species when food is not limiting. Because of their larger size, toucans may require more nutrients for survival and therefore need tighter control over limited food resources in the wet season. Studies examining toucan dominance, foraging behavior, and food availability in the wet season could evaluate the effect of seasons on community structure.

The high incidence of displacement of Aracaris and Keel-

billed Toucans by Chestnut-mandibled Toucans suggests that a dominance hierarchy may exist among these three species. These species have similar diets (Stiles and Skutch 1989), and it may be more efficient for Chestnut-mandibled Toucans to exclude close competitors than to expend energy excluding all frugivores in the avian community.

To our knowledge, there have been no previous Dartmouth studies of the potential role of toucans in structuring the frugivorous bird community at La Selva. Our study provides a set of base-line data on toucans, including flock size and behavior, which may be used for future studies involving toucan species.

LITERATURE CITED

- Stiles, F. G. and Skutch, A. F. 1989. A guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, New York, USA.
- Janzen, D. H. 1983. *Ramphastos swainsonii*. Pages 603 - 604 in D.H. Janzen, editor. Costa Rican Natural History. University of Chicago Press, Chicago, Illinois, USA.