

POSITIVE FEEDBACK BETWEEN *ACACIA COLLINSII* AND  
*PSEUDOMYRMEX SPINICOLA* COLONIES

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*Abstract:* Mutualisms play prominent roles in tropical ecosystems. However, the maintenance of obligate mutualisms is still poorly understood. In this study, we looked for signs of positive feedback between two common mutualists in a tropical dry forest in Costa Rica: *Acacia collinsii* trees and *Pseudomyrmex spinicola* ant colonies. To examine the mutual benefits experienced by plants and ants, we assessed the leafiness of each plant as well as the size of the associated ant colony. We found a weak positive correlation between plant productivity and ant colony size, but no correlation between plant productivity and ant colony response to simulated herbivory. Finally, we observed an eight-fold greater recruitment of *P. spinicola* to the trunk of the plant as compared to the auxiliary branches in response to disturbance.

*Key Words:* mutualism, neotropic, Costa Rica, Palo Verde, dry forest

INTRODUCTION

Mutualisms are reciprocally beneficial inter-specific interactions that are ubiquitous in nature, especially in tropical environments (Bronstein, 1998). The evolution and ecology of mutualistic interactions between ants and plants has been particularly well studied because ants are both very common and prone to entering mutualisms (Bronstein, 1998). A common ant-plant mutualism between the tree *Acacia collinsii* (Fabaceae) and the ant species *Pseudomyrmex spinicola* (subfamily Pseudomyrmecinae) occurs in the Costa Rican tropical dry forest (Janzen, 1966). While the costs and benefits of this obligate mutualism are well studied, the

mechanisms through which the interaction evolved and how and why it continues to flourish have not been well-studied (Bronstein, 1998). Although it is often assumed that the evolution and persistence of mutualisms involve a positive feedback cycle, most studies focus solely on the costs and benefits of the interaction for one partner in the relationship (Bronstein, 1994). In this study, we tested whether there was evidence of positive feedback in the obligate mutualism between *A. collinsii* trees and *P. spinicola* colonies.

*Acacia collinsii* provides ants with shelter in the form of hollowed thorns and food in the form of extrafloral nectaries and lipid-rich Beltian bodies (Janzen, 1966). In

return, *P. spinicola* protects *A. collinsii* by attacking herbivores and clearing away competing vegetation (Janzen, 1966). *Acacia* species without thorns must invest a greater amount of metabolic energy in secondary compounds (Zuchowski, 2005). Ant mutualisms allow the *Acacia* to invest in Beltian bodies and nectaries as indirect methods of defense, rather than secondary compounds, some of which may be more metabolically costly (Zuchowski, 2005). Thus, the mutualism between ants and acacias may result in a positive feedback cycle: well-protected trees may grow larger with more leaves (Janzen, 1966) and therefore more resources to provide food and shelter for ants, subsequently increasing ant colony size. Additionally, in dry climates, acacias drop their large leaves and only produce small young leaves containing Beltian bodies to feed their obligate ants (Janzen, 1966). The number of small young leaves produced is therefore a representation of the energy investment the acacias put toward maintaining their ant colony with extra lipids.

We examined positive-feedback patterns in the mutualism between *A. collinsii* and *P. spinicola* by evaluating the relationships between tree leafiness, ant colony size, and ant defensive behavior. We hypothesized that a positive feedback between ants and acacias

would result in positive correlations between tree leafiness and ant colony size. In addition, ants might more aggressively defend trees that are leafier, and thus more valuable to the ants (Burnaford et al., 1992). Thus, we also considered the hypothesis that trees might be leafier if ants were simply more aggressive, and not necessarily greater in number.

Specifically, we predicted that (1) leafier trees would have larger ant colonies and (2) ant colonies on leafier trees would defend their trees more aggressively. Finally, during our field observations, we noticed that ants had a tendency to respond in greater numbers to the trunk of the tree than the branches of the tree during simulated herbivory. We tested this pattern by comparing ant behavioral response to simulated herbivory on tree trunks and auxiliary branches.

## METHODS

We conducted our study at Palo Verde National Park, located in the Guanacaste province of northwestern Costa Rica. This 20,000-hectare park is a seasonally dry tropical forest dotted with limestone cliffs, bordered by wetland vegetation along the Tempisque River.

We haphazardly selected 38 *A. collinsii* trees that were colonized by *P. spinicola*, located 1-10 m from

either side of the dirt road leading to the Palo Verde field station. We counted the number of leaves on one 30 cm section of branch per tree (hereafter referred to as tree leafiness) as an estimate of a tree's potential energy available for maintaining an ant colony. We counted the initial number of ants on the branch segment and then simulated herbivory by tapping the branch segment for 10 sec. After tapping the branch, ants entered the branch from the thorns. We counted the total number of ants on the 30 cm branch segment after simulated herbivory as a measure of the total ant colony size. The final number of ants on the 30 cm branch segment reflects the initial number of ants on the branch, as well as those in the thorns. We measured the ant behavioral response as the change in ant numbers 10 sec after the simulated herbivory. To justify using a single branch measurement to represent the entire tree, we tested the variation in ant response between two auxiliary branches on the same tree. On 10 trees, we chose two auxiliary branches from the same section of the tree and sampled ant colony size and response to simultaneous disturbance simulations, as described above. For all trees, we recorded the time of day that the simulated herbivory was conducted.

To test if ant response was greater on the trunk of the tree than

the auxiliary branches, we haphazardly sampled 10 trees that were 1-2 m tall. We chose a 30 cm section on the main trunk of each tree and a 30 cm section on an auxiliary branch above the trunk segment and measured ant colony size and response to simultaneous disturbance simulations, as described above.

We tested the relationships between acacia leafiness and our estimates of ant colony size and ant response to simulated herbivory with correlation analyses. We also tested the correlation between time of day and ambient ant numbers to see if the response of ants varied over the course of our data collection period (0800 – 1100). We performed a two-tailed, paired t-test to determine if there was a difference in ant response to tapping between two branches within a tree. We performed a one-tailed, paired t-test to test our *a priori* hypothesis that ant response would be greater on the trunk than on an auxiliary branch.

## RESULTS

The number of ants present after tapping was weakly positively correlated with acacia leafiness (leaves per 30 cm of branch;  $r = 0.30$ ,  $n = 37$ ,  $P = 0.07$ ; Fig. 1). However, there was no relationship between leafiness and number of ants responding to the branch after tapping ( $r = 0.02$ ,  $n = 37$ ,  $P = 0.90$ ; Fig.

2). Thus, ant colonies in leafier trees were larger, but did not respond to simulated herbivory more aggressively.

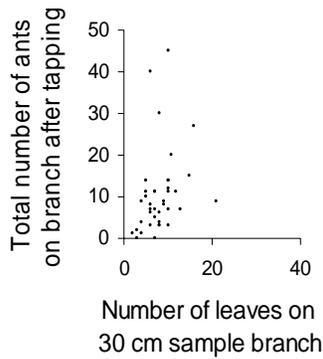


Figure 1. Correlation between the number of *Acacia* leaves on a 30 cm sample branch and number of ants on the branch after tapping to simulate herbivory (n = 38 trees). Each point represents a different tree.

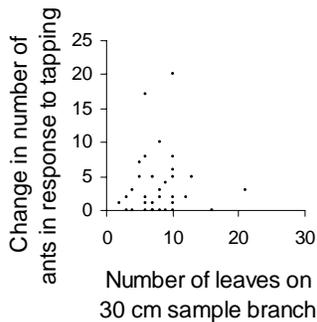


Figure 2. The density of *Acacia collinsii* leaves (number of leaves on 30 cm sample branch) and change in number of *Pseudomyrmex spinicola* ants on a branch in response to tapping. Each point represents a tree (n = 38 trees).

There was no difference between ant response to the tapping on two branches within a tree (paired- $t_9 = -0.37$ ,  $P = 0.72$ ), suggesting that one branch was a representative sample of the entire tree. However, there was a strong

positive correlation between the initial number of ants and the time of day; initial ant activity increased as the morning progressed ( $r = 0.58$ ,  $n = 37$ ,  $P < 0.01$ ). Finally, the mean number of ants responding to tapping on the trunk was eight times greater than the mean number of ants responding to the auxiliary branch (paired- $t_9 = 5.86$ ,  $P < 0.01$ ; Fig. 3).

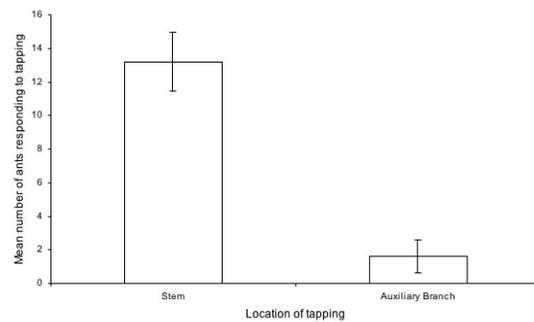


Figure 3: Mean number of *Pseudomyrmex spinicola* ants responding to tapping on the trunk (n = 10 trees) and on the auxiliary branch of *Acacia collinsii* (n = 10 trees). Error bars represent  $\pm 1$  SE.

## DISCUSSION

In our study of the potential positive feedback between *A. collinsii* and *P. spinicola*, we found a positive correlation between acacia leafiness and ant colony size. Our first hypothesis, that *P. spinicola* colony size would be positively correlated with leafier trees, was supported; leafier trees had more ants. Although the leaf-ant relationship was weak, it corroborates the hypothesis that there may be positive feedback between *P.*

*spinicola* colony size and *A. collinsii* leafiness. To further elucidate the observed correlation, future studies should attempt to separately discern the effect of leafier *A. collinsii* on *P. spinicola* colony size and the effect of *P. spinicola* colony size on *A. collinsii* leafiness. If it could be demonstrated that leafier trees cause bigger ant colonies, and that bigger ant colonies cause bigger trees, the degree of this positive feedback cycle could be quantified.

Our second hypothesis, that the *P. spinicola* colonies would defend leafier trees more aggressively, was not supported; there was no relationship between the number of ants after a disturbance and the number of leaves, both on the sample branch. However, we may have failed to detect a response because we only sampled auxiliary branches, and our third experiment demonstrated that ants responded mainly towards the main trunk of the plant. In other words, we may have failed to detect a correlation between tree leafiness and ant aggressiveness, not because no such correlation exists, but because the trunk effect overwhelmed our measurements at the auxiliary branch.

The ants may more actively defend the trunk because that may be where the reproductive future of the colony is located. After cutting open three large thorns from the trunk of three separate *A. collinsii*

trees, we found large quantities of *P. spinicola* eggs, larvae, pupae, and winged adults. Quantifying the correlation between the location of the juvenile *P. spinicola* and the location of the *P. spinicola* response to simulated herbivory may therefore be a fertile ground for future research. A subsequent study found that the large, central thorns of the tree contained the ant eggs, larvae, pupae and the queen of the colony, while the smaller thorns on auxiliary branches did not, further supporting our hypothesis that ant response will be greatest to the trunk of *A. collinsii* (Isbey et al. SIFP1 2007).

Our study supports the hypothesis that the ant-acacia mutualism exhibits positive feedback. This evidence for positive feedback between ants and acacias may help explain how mutualistic interactions are maintained. If mutualistic partners are tightly linked through positive feedback, then declines in one partner could result in two outcomes. First, the beneficial partner may be able to help a declining partner regain strength. Alternatively, if the health of the second partner is closely linked to the first, the second might weaken as well, leading to a more rapid decline of the entire mutualistic relationship. Future studies should experimentally test the strength of the mutual benefits between *A. collinsii* and *P. spinicola* to determine if the positive correlative

patterns we observed are causal and how quickly partners will respond to changes in each others abundance.

*belti*) by their obligate mutualist host *Acacia collinsii*. *Dartmouth College Biology FSP*, pp. 4-6.

#### LITERATURE CITED

Bronstein, J. L., 1994. Our current understanding of mutualism. *The Quarterly Review of Biology*, 69 (1): 31-51.

Bronstein, J. L. 1998. The contribution of ant-plant protection studies to our understanding of mutualism. *Biotropica*, 30 (2): 150-161.

Bronstein, J.L. 2001. The costs of mutualism. *American Zoology*, 41:825-839.

Burnaford, JL, Gunderson EW, Ko, JV, Shabel, AB, and Wooley SA. 1992. Differential nectar production offered to two species of ants (*Pseudomyrmex ferruginea* and *P.*

Isbey S, Lei S, Haynor S, and Gorbakin, C. 2007. The colony architecture of *Pseudomyrmex spinicola* in the ant-plant *Acacia collinsii*. *Dartmouth Biology FSP*, unpublished MS.

Janzen, DH. 1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution*, 20:249-275.

Palo Verde National Park. Organization for Tropical Studies. 8 Jan 2007. <http://www.ots.ac.cr/en/paloverde/>

Zuchowski, Willow. 2005. *A Guide to the Tropical Plants of Costa Rica*. Distribuidores Zona Tropical, S.A: Miami, pp. 270-1.