

APPLYING OPTIMAL DEFENSE THEORY TO ANT-ACACIA MUTUALISMS

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Abstract: Optimal defense theory predicts greater resource allocation to the defense of plant tissues that are more valuable to plant fitness. We tested an extension of this theory to indirect mechanisms of plant defense, namely the mutualism between *Acacia collinsii* and three species of its ant colonizers. We observed ant response to simulated herbivory on fruits, flowers, and leaves. We tested acacia defensive allocation by studying which structures were more highly defended by ants. Based on optimal defense theory, we hypothesized that ants would defend fruits and flowers more heavily than leaves due to their reproductive value for plants. Prior to trials simulating herbivory, the baseline (control) conditions had significantly more ants present on undisturbed leaves than on undisturbed flowers. During treatment trials simulating herbivory, there was no significant difference in ant response between leaves and reproductive structures (flowers or fruits). Possible explanations for our results include 1) ants may only respond to direct threats to the fitness of their colony, 2) herbivory was poorly simulated, and 3) optimal defense theory may not apply to indirect defenses. We conclude that while ants mutualistically protect acacias from leaf herbivory, they do not preferentially defend reproductive structures, as optimal defense theory would predict.

Key Words: *Acacia collinsii*, *plant defense*, *Pseudomyrmex spinicola*, *Pseudomyrmex flavicornus*, *Crematogaster brevispinosa*

INTRODUCTION

Optimal defense theory (ODT) for plants states that a plant will allocate defensive resources to tissues based on the value of the tissue to plant fitness, the probability of damage to that structure, and the ecological and allocation costs of defending the tissue. ODT is the result of studies on secondary compound distribution within and among plants (McKey, 1974) and was elaborated on by studies of plant responses to herbivory (Zangerl and Rutledge, 1996). Because reproductive structures are

often more important to plant fitness than leaves, secondary compounds are expected to be found in higher concentrations near and in plant reproductive structures (McKey, 1974).

ODT has been used to understand the distribution of chemical defenses in plants (McKey, 1974). However, some plant species rely on indirect defenses, such as predators of herbivores, as a source of protection against herbivory. For example, *Acacia collinsii* (Fabaceae) relies on ants to deter herbivores (Janzen, 1983). Because the presence of ant mutualists on acacias relieves

some of the defensive burden, plant secondary compound production decreases and plant fitness increases after ant colonization (Janzen, 1966). Here, we extended predictions of ODT to indirect defense mutualisms to ask whether predictions from ODT could be used to understand how plants defend different tissue types. In only a limited number of cases have predictions from ODT been successfully applied to indirect plant defenses, such as ant mutualists (Wackers and Bonifay, 2004).

We examined acacia defensive resource allocations by studying which plant structures ant mutualists defend most strongly. Assuming that acacia fruits and flowers are highly valuable structures to the tree for reproduction, we predicted, under ODT, that ants would defend these structures more strongly than they would leaves.

METHODS

Study system.

Acacia collinsii (hereafter referred to simply as acacias) benefit from a mutualistic relationship when colonized by some ant species. Eight ant species in the Guanacaste Province of Costa Rica are known to enter in this mutualism. Each individual tree is colonized by one species. Acacias provide ants with thorn habitat, nectar, and Beltian

bodies in exchange for protection against herbivores and competing plants. We focused on trees colonized by three common ant species, *Pseudomyrmex spinicola*, *P. flavicornus*, and *Crematogaster brevispinosa*. Ant species vary in the anti-herbivore protection they provide to acacias; *Pseudomyrmex spinicola* is the most aggressive at defending the plant (Janzen, 1983).

Field methods.

We collected data midmorning on 8 January, 2007, at Palo Verde National Park in the Guanacaste region of Costa Rica. We haphazardly selected 18 acacia trees with leaves and either pods or flowers. Each tree contained one of the three species of ant mutualist. To estimate plant defense to different tissue types, we quantified ant activity following simulated herbivory to leaves, pods, or flowers.

Before simulating herbivore behavior, we ran control trials for one leaf and one reproductive structure (either a pod or a flower). We observed the structures for two minutes at ten second intervals, noting the number of ants on both structures and on the inter-nodal branch area, also recording the ant species present (Figure 1). The control was used to determine the normal activity levels of ants on each of the three structures.

We simulated herbivore behavior by tapping simultaneously

on one leaf and one reproductive structure located on different branches of the tree for one minute. We observed the ant activity in the area for one additional minute after tapping. Response variables recorded for the treatment were the same as for the control trials.

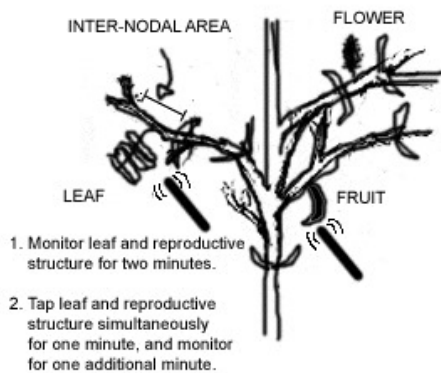


Figure 1. We monitored ant activity on acacia plant structures (flower, fruit, and leaf) across (1) control and (2) treatment methods.

Because observations of the leaves and reproductive structures were paired for each tree, we used paired t-tests to compare the mean (square-root transformed) and maximum number of ants on leaves to their numbers on reproductive structures.

To determine where acacias place incentives for their mutualists, the number of nectaries was counted at the base of haphazardly selected flowers, pods, and leaves on 17 trees. We sampled up to three replicates of each structure present per tree. We

calculated the mean number of nectaries for each structure.

RESULTS

In the control treatment, the mean number of ants on leaves was 140% higher than the mean number of ants on flowers ($t_7 = 2.54$, $P = 0.039$, Figure 2). Moreover, the maximum number of ants on leaves was 84% higher than the maximum number of ants on flowers ($t_7 = 5.18$, $P = 0.0013$, Figure 3). However, there was no significant difference between leaves and pods for mean ($t_8 = 1.18$, $P = 0.27$) or maximum number of ants ($t_8 = 1.20$, $P = 0.26$).

In the herbivore (tapping) simulation treatment, there were no significant differences in mean and maximum numbers of ants between leaves and flowers and between leaves and pods (Table 1).

In our nectary survey, the bases of leaves contained a mean \pm 1 SD of 2.61 ± 0.46 nectaries. No nectaries were present on the bases of flowers or fruits.

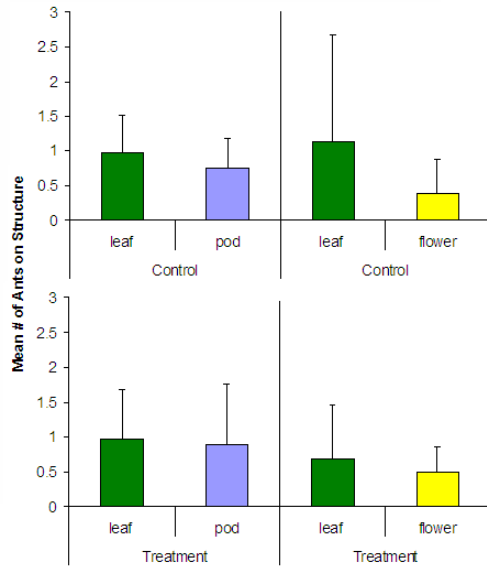


Figure 2. Mean number of ants counted on acacia leaves and flowers or leaves and pods for (a) control and (b) treatment trials. Error bars show SE. In both control and treatment trials, N = 8 paired leaves and flowers; N = 10 paired leaves and pods.

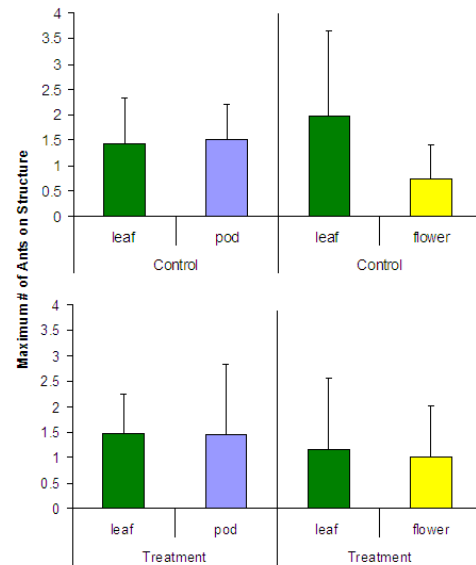


Figure 3. Maximum number of ants counted on acacia leaves and flowers or leaves and pods for (a) control and (b) treatment trials. Error bars show SE. Sample sizes as in Figure 2.

Table 1. Results of paired t-tests in the treatment trial. Each pair of acacia structures (leaves/flowers, leaves/pods) is shown for each variable.

Treatment	Mean \pm SE	t-ratio	P > t	df
Mean # Ants: Flowers and Leaves	0.49 \pm 0.84	0.60	0.566	7
Mean # Ants: Pods and Leaves	0.09 \pm 0.26	0.38	0.923	8
Max # Ants: Flowers and Leaves	0.38 \pm 1.76	0.31	0.762	7
Max # Ants: Pods and Leaves	0.50 \pm 0.76	0.099	0.923	8

DISCUSSION

ODT predicts that tissues more closely tied to plant fitness, such as flowers and fruits, should be more heavily defended. However, ODT has rarely been applied to indirect plant defenses. Our data failed to support the hypothesis that more ants would be found on the

flowers and pods of acacia trees than leaves after simulated herbivory. Tapping on plant structures did not cause preferential defense, but when undisturbed, ants spent more time on leaves than flowers. These results suggest different priorities for the ant and the acacia. While the flowers and pods are important to acacia reproduction, the leaves are

probably more important to the ants because they contain nectaries and Beltian bodies on which the ants feed. Because the ants and acacias likely value leaves and reproductive structures differently, ODT may not be applicable to indirect defense mutualisms in this system.

A number of mechanisms, none of which are mutually exclusive, may explain our results. First, acacias may discourage ants from patrolling flowers to decrease the number of potentially negative ant-pollinator interactions (Ghazoul, 2001). Similarly, ants may be less abundant on fruit pods to decrease the possibility of deterring mutualist seed dispersers (Carey et al., 2005). Second, our initial assumption that fruits and flowers would be more closely tied to plant fitness may have been erroneous for this particular species. ODT was developed based on studies of short-lived species (McKey, 1974). Because acacias are long-lived species, annual plant reproduction may be less important to their fitness than postulated by ODT. Third, our simulation of herbivore presence may have been too vigorous, and therefore unrealistic. Given the size of the tapping implement and the force with which we tapped, the ants may have been overwhelmed and unable to respond as they would to a real herbivore. Four out of the five main acacia herbivores are larvae that feed specifically on leaves, indicating that

ant abundance on the leaves during the control trials could be a form of preemptive defense (Janzen, 1983). Thus, the threat of herbivory on leaves may be higher and more detrimental than originally expected.

Another limitation of our study is an incomplete consideration of optimal defense theory's premises. Our study contained a bias toward the premise of tissue value and lacked investigation into probability of damage and cost of defense, two of the three facets of ODT. To explore the importance of the other two tenets, potential areas of further study include experimental manipulation of nectar availability on different tissue types and investigation into potential deterrent compounds in pods and flowers (Ghazoul, 2001). Sampling damage on leaves, flowers, and pods to determine herbivory levels would also help determine which structures are at the highest risk of damage.

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