

DEFENSIVE RESPONSE OF MUTUALISTIC ANTS TO SIMULATED MAMMALIAN HERBIVORY ON *ACACIA COLLINSII* AND *A. CORNIGERA*

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Abstract: Differences in the ant-acacia mutualisms between *Acacia collinsii* and *A. cornigera* have not been compared directly, but a previous study in the Palo Verde National Park suggested that the mutualism was dysfunctional in *A. cornigera*. We compared the response of ant colonies between *A. collinsii* and *A. cornigera* after simulated mammalian herbivory. As predicted, ants attacked more frequently on *A. collinsii* than on *A. cornigera*, a trend that was marginally significant in spite of low sample size dictated by the rarity of *A. cornigera*. Hybridization of these acacia species may have occurred in the study area, reducing observed differences in ant behavior.

Key Words: palatability, hybridization, Beltian bodies

INTRODUCTION

Aggressive ants occupy two species of acacia trees: *Acacia collinsii* and *A. cornigera*. Both species occur in Palo Verde, Costa Rica, but *A. cornigera* is much less common. Resources provided to the ants include carbohydrates in extrafloral nectaries, lipids in Beltian bodies, and shelter for the colony to live and rear larvae in hollowed thorns (Janzen, 1974). Several species of aggressive ants inhabit acacias in Palo Verde (*Pseudomyrmex flavicornis*, *P. spinicola*, and *P. nigrocincta*), and ant colonies aggressively defend their host trees both from herbivores and other ants.

A previous study suggested that the mutualism between *A. cornigera* and its resident ants has failed, resulting in trees that

continue to provide habitat and nutrients to the ants without receiving the benefit of ant defense (Bates et al. 2006). However, that study did not include comparative sampling of *A. collinsii* with *A. cornigera*.

We hypothesized that aggressive ant colonies would defend *A. collinsii* more effectively than *A. cornigera*, and we tested this by simulating mammalian herbivore attack on both species on the same day in the same habitats.

METHODS

Our experiment was conducted from 0725-1030 on January 12, 2008, within ca. 200m of the OTS field station at Palo Verde, on both sides of the main access road. We used every available *A.*

cornigera within the study area, but their rarity limited our sample size to five. We chose five *A. collinsii* that were of comparable size to the *A. cornigera* sampled, and nearest to them.

Branches within the approximate height range accessible to cattle were selected at random, and cattle herbivory was simulated by tearing off leaves with gloves, a modification of the technique used by Barger et al. (2005). One compound leaf was removed every 10 seconds for up to 60 seconds (6 leaves removed). We recorded the time to first arrival of an ant to the glove, and the time to first bite or sting. At time of first bite or sting, leaf removals were stopped, and if no ants had arrived, we waited up to 30 seconds more (90 seconds total) for ants to respond. We scanned each tree for one minute and recorded the number of leaves with mature Beltian bodies. We measured each tree's height, the long axis of the projected crown area, and the width perpendicular to the long axis. An index of projected canopy area was calculated as the product of these two measures. Ant species from each tree were then collected and identified.

RESULTS

TABLE 1: Attack frequencies of resident ants on *A. collinsii* and *A. cornigera* at Palo Verde National Park, Costa Rica

	No. Attacks	No. failures to attack	Total No. Ant Species Sampled
<i>A. cornigera</i>	2	3	5
<i>A. collinsii</i>	5	0	5
Total # of outcomes	7	3	10

Every herbivore simulation on *A. collinsii* generated an attack, compared to only 40% for *A. cornigera*. Each tree was inhabited by a single ant species, suggesting that these ant colonies defend against other ant colonies, if not against herbivores.

Time to first attack was not linearly related to projected canopy area ($F=0.77$, $df = 1, 10$, $p=0.42$) or height ($F=0.475$, $df=1, 10$, $p=0.52$). Of the trees sampled, 80% had one or fewer Beltian bodies, and the number of bodies was not linearly related to time to first attack ($F=0.16$, $df = 1, 6$, $p=0.71$).

The probability of attack in *A. collinsii* may be greater than in *A. cornigera* (Table 1, Fisher's exact test, $p=.083$). More replication would be necessary to confirm this difference.

TABLE 2: Ant species occupying *A. collinsii* and *A. cornigera* at Palo Verde, Costa Rica

Ant species	Acacia species	
	<i>A. collinsii</i>	<i>A. cornigera</i>
<i>P. flavicornis</i>	1	3
<i>P. nigrocincta</i>	2	0
<i>P. spinicola</i>	2	2

DISCUSSION

The mutualism between ants and *A. cornigera* did not appear as functional as that with *A. collinsii*. Two of the aggressive ant species that occur in *A. cornigera* (*P. flavicornis*, *P. spinicola*) also frequently occupy *A. collinsii* trees (Table 2). Bates et al. (2006) showed that *P. flavicornis* was far less aggressive when inhabiting *A. cornigera*. Our data support that inference, with 60% of our *A. cornigera* trees showing no aggressive response to herbivory.

The absence of aggressive response in *A. cornigera* for ant species that aggressively defend *A. collinsii* is puzzling, and further suggestive of a dysfunctional mutualism in *A. cornigera*.

In contrast to these findings, ants residing on both tree species had similar response times when ants defended aggressively. These apparently inconsistent results may be reconciled by future studies with larger sample sizes.

It is possible that *A. cornigera* is not an obligate mutualist with ants. If so, it may be less palatable to mammalian herbivores than *A. collinsii*. *A. collinsii* lacks secondary compounds (Janzen, 1977), but the palatability of *A. cornigera* has not been evaluated.

Ant acacias occasionally hybridize (Ebinger and Seigler 1992, Janzen 1974). In our samples near the

road, there appeared to be a continuum of morphological traits in the ant acacias, rather than the distinct species characteristics of *A. collinsii* and *A. cornigera* that were apparent in trees near the marsh. Hybridization between the species could have resulted in intermediate ant behaviors in some of our samples, reducing differences between the acacia species in our experiment.

LITERATURE CITED

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