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Do facultative and obligate mutualist ants provide equal protection for their acacia hosts?

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Abstract: Ants and acacias provide a classic example of a mutalism in which one species gains food and the other protection. Some ant species, such as *Pseudomyrmex spinicola*, are obligate mutualists with acacias such as *Acacia collinsii*, while others, such as *Crematogaster brevispinosa*, have a more facultative association. Because *C. brevispinosa* is not totally dependent on *A. collinsii*, we hypothesized that *C. brevispinosa* and *P. spinicola* would not be equal defenders of *A. collinsii*. We tested this hypothesis by measuring herbivory on acacias occupied by the two ant species, ground cover under those acacias, and the response of each ant species to temporary physical disturbance. We found no significant difference in herbivory between acacias occupied by the two ant species, suggesting they are equally effective in defending against herbivores. We found that both ant species responded similarly to temporary physical disturbance, further supporting their equality as host defenders. However, *C brevispinosa* exhibited a higher ambient patrol rate than *P. spinicola*, and acacias occupied by *P. spinicola* had less ground cover. Our findings suggest that the facultative mutualist and the obligate mutualist provide comparable levels of host defense, although their defensive strategies appear to differ.

Key Words: Acacia collinsii, Crematogaster brevispinosa, *herbivory, mutualism,* Pseudomyrmex spinicola

Introduction

Mutualistic relationships vary greatly in the degree to which species depend on and protect one another. In obligate symbiotic relationships, each species involved depends on the other for survival. These obligate mutualisms, however, may be vulnerable to changing conditions or colonization by other species. Facultative mutualists that can survive in a variety of situations may not provide the same benefits to their hosts as obligate mutualists.

A mutualistic relationship has evolved between acacia trees and certain ant species. The acacia plants provide shelter in their thorns for the ants and supply them with food: protein from Beltian bodies and carbohydrates from extra-floral nectaries (Janzen 1983). Acacias in Palo Verde National Park in Costa Rica host several species of acacia ants. Of three species of obligate mutualist ants, which occur only in association with one or more species of acacia, *P. spinicola* is the most aggressive in defending its host (Janzen 1983). A facultative mutualist, *Crematogaster brevispinosa*, also occurs on acacias, but has likewise been found in association with other plant species (Janzen 1983).

The degree to which *C. brevispinosa* protects its acacia host remains unclear. *C. brevispinosa* colonizes older trees and shows aggressive defense against recolonization by *P. spinicola* (Janzen 1983). Foote et al. (2000) found that *C. brevispinosa* colonizes tree stands to the exclusion of other species. Hanke et al. (1999) reported that *C. brevispinosa* also exhibits aggressive behavior against conspecifics from other acacias. These aggressive behaviors imply self-preservation, but they do not necessarily suggest effective defense of their host. Studies have not yet determined whether the facultative mutualist *C. brevispinosa* protects its host trees to the same degree as the obligate mutualist *P. spinicola.*

We hypothesized that the facultative mutualist *C. brevispinosa* and the obligate mutualist *P. spinicola* defend their host trees with different degrees of effectiveness. Based on this hypothesis, we predicted that trees occupied by *P. spinicola* would show less evidence of herbivory and less ground cover around their trunks than those occu pied by *C. brevispinosa*. Base areas free of ground cover are thought to result from ants clearing away vegetation (Janzen 1983). We also predicted that *P. spinicola* would show a greater response to temporary physical disturbance of their hosts than would *C. brevispinosa*.

Methods

We conducted our experiment in Palo Verde National Park, Guanacaste Province, Costa Rica. We sampled 20 acacia trees, 10 inhabited by *P. spinicola* and 10 inhabited by *C. brevispinosa*. The trees were located along the entrance road to the park within 3 km east of the OTS field station. We chose trees that were a minimum of 2 m high and had branches with live leaves at a minimum of 1 m high.

We first quantified the levels of defense provided to the trees by the two ant species. We measured damage from herbivory on each acacia tree by examining two leaves at the ends of two ~1 m high branches on opposite sides of each tree and counted the number of damaged and undamaged sub-leaflets on each leaf. We calculated the percent damage on each leaf and analyzed these data using a t-test. We measured ground cover under each tree within a circle of radius 0.5 m as either 0-50% or 51-100%, and compared differences between acacias occupied by the two ant species with a X^2 analysis.

To examine patrolling rates of each ant species we counted the number of ants crossing an imaginary line around a branch approximately 1 cm in diameter and 1 m high near the trunk during a 30 s interval. We then disturbed each branch by continually tapping on it for 15 s, and then counted the number of ant crossings during the following 30 s interval. Differences in mean pre- and post disturbance patrolling activity between species and between mean pre- and post disturbance patrolling activity within each species were analyzed with t-tests. Data are reported as means ± SE.

Results

Herbivory rates were 27 ± 6% for acacias occupied by *P. spinicola* and 32 ± 6% for acacias occupied by *C. brevispinosa* (Fig. 1). These rates of herbivory did not differ significantly ($t = -0.66$, $df = 15$, $P = 0.56$).

Sixty percent of the acacias inhabited by *P. spinicola* had 0-50% cover around their bases compared to only 10% for the acacias inhabited by *C. brevispinosa* (Fig. 2). The proportion of ground cover at the base of trees inhabited by *P. spinicola* and *C. brevispinosa* differed significantly ($X^2 = 5.95$, $df = 1$, $P = 0.02$).

Pre-disturbance activity was greater for *C. brevispinosa* than *P. spinicola* with 31.8 ± 2.64 ant crossings per min and 1.0 ± 0.22 ant crossings per min, respectively (Fig. 3). These values in pre-disturbance (ambient) rates were differed significantly between species ($t = 5.81$, $df = 18$, $P < 0.001$). Within each species, the difference between pre- and post disturbance activity levels was 31.8 ± 15.04 for *P. spinicola* and 54.8 ± 12.62 for *C. brevispinosa*. These changes in response levels were highly significant for *P. spinicola* ($t = 8.35$, $df = 18$, $P < 0.001$), but not for *C. brevispinosa* ($t = 1.12$, $df = 18$, $P = 0.28$).

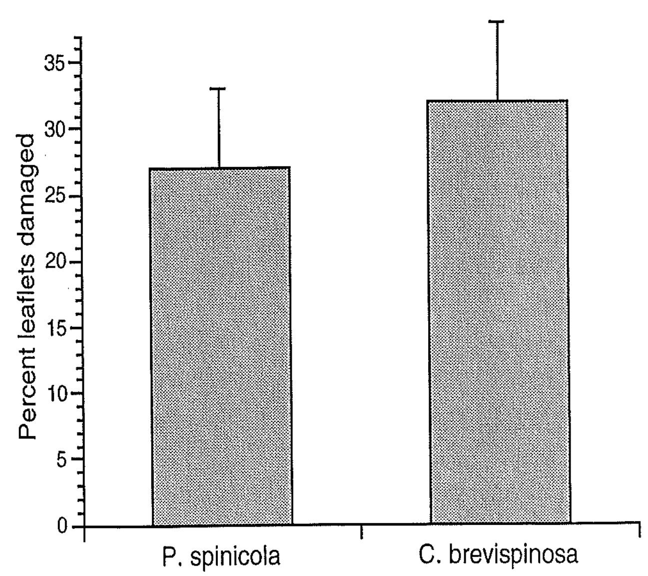

FIG. 1. Herbivory levels on leaflets on *A. collinsii* trees inhabited by *P. spinicola* and *C. brevispinosa*. Data represent means ± SE. n = 10 for each species.

Discussion

We found similar patrol levels in *C. brevispinosa* and *P. spinicola* after a disturbance. This finding suggests that these species are both good defenders of their hosts, contrary to our expectations. Additionally, our findings indicate that levels of herbivory on acacias with *P. spinicola* and *C. brevispinosa* were similar, suggesting that these ant species are equally effective at defending their hosts against herbivores. Consistent with our prediction, *P. spinicola* removed more ground cover around the base of its host trees than did *C. brevispinosa*. Although this activity does not appear to have any defensive value against herbivores, the removal of vegetation is thought to reduce competition by other plants with the acacia (Janzen 1983).

Although *P. spnicola* and *C. brevispinosa* exhibited unequal ambient patrol levels, this behavior apparently did not affect defense against herbivory, since herbivory rates across species were equal. Instead, unequal ambient patrol activity may reveal a strategic difference between the species in their defense responses. *Pseudomyrmex spinicola* has been reported to secrete a chemical cue when responding to disturbance (Janzen 1983). The rapid communication facilitated by such a cue may allow *P. spinicola* to reduce its ambient patrol activity. The role of chemical cues in *C. brevispinosa* defense response has not been tested, but may provide a possible explanation for its higher ambient patrol rate.

Our findings suggest that a facultative mutualist, *C. brevispinosa*, and an obligate mutualist, *P. spinicola*, can provide comparable levels of host defense, despite differences in dependency on their host. Further exploration of *P. spinicola* and *C. brevispinosa* communication mechanisms and distributions on *A. collinsii* is needed to enhance our understanding of host defense resulting from facultative and obligate mutualistic relationships.

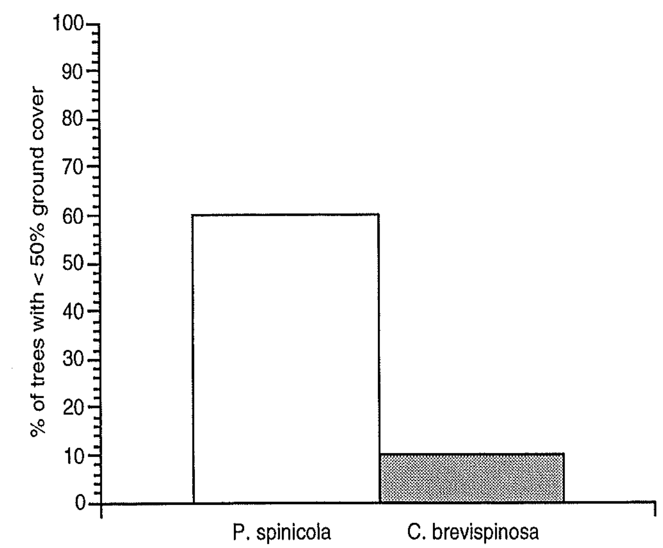

FIG. 2. Percent of *A. collinsii* inhabited by *P. spinicola* and *C. brevispinosa* with < 50% ground cover within a 0.5 m radius of their trunks. n = 10 for each species.

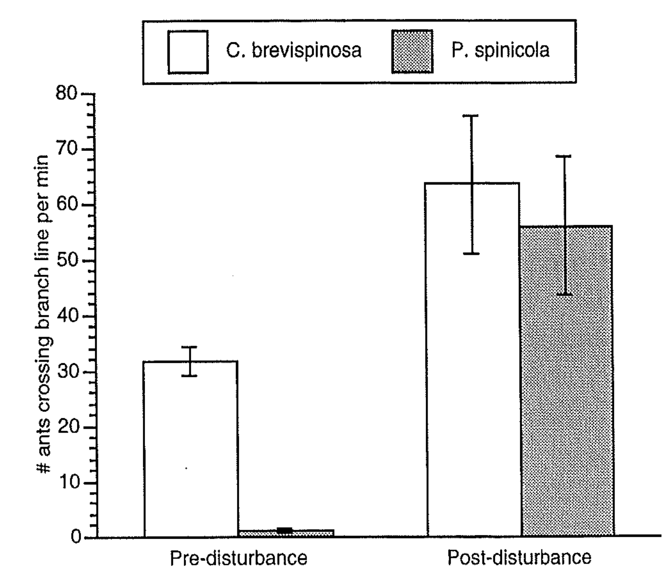

FIG. 3. Pre and post-disturbance patrol rates for *C. brevispinosa* and *P. spinicola* on *A. collinsii* host trees. Data represent means ± SE, n = 10 for each species.

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