COLONIZATION AND DEFENSIVE ABILITIES OF ACACIA ANT SPECIES IN AN EARLY SUCCESSIONAL DRY TROPICAL FOREST

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Abstract: The ant species *Pseudomyrmex flavicornis*, *P. spinicola*, and possibly *Crematogaster brevispinosa* occur in a symbiotic relationship with *Acacia collinsii*. *C. brevispinosa* has been reported to occupy mostly dead or dying acacias (Janzen 1983), but Ermentrout et al. (2003) found that it was one of the two most common ant species on acacias in an early successional site. We hypothesized that *C. brevispinosa* may be a good colonizer of young acacias but a poor defender of their host plants, resulting in their disappearance in late successional stages. We quantified (1) the presumed colonizers of acacias by examining which ant species occupied young trees (defined as those ≤ 1 m tall), and (2) the defensive abilities of each ant species. *P. spinicola* was the most common ant species on small acacias (60%) with *C. brevispinosa* the second most common (31%). In our behavioral test, we found no difference between the defensive abilities of *C. brevispinosa, P. spinicola*, and *P. flavicornis* in response to disturbance. Thus, prevalence of *C. brevispinosa* in this early successional dry tropical forest is still largely unexplained, and further studies are needed to clarify its relationship with *A. collinsii*, as well as its patterns of occurrence and distribution.

Key words: Acacia collinsii, *defensive abilities*, Crematogaster brevispinosa, Pseudomyrmex flavicornis, Pseudomyr-

INTRODUCTION

Acacia collinsii exists in a mutualistic relationship with several species of ants including *Pseudomyrmex flavicornis*, *Pseudomyrmex spinicola*, and possibly *Crematogaster brevispinosa*. *P. flavicornis* appears to occupy acacias more frequently in open sun, *P. spinicola* occurs across all habitats, and *C. brevispinosa* has been reported to occupy mostly dying or dead acacias, presumably after the originally colonizing ant species has abandoned the tree (Janzen 1983:762). Assuming that a later successional forest should contain a higher proportion of dead or dying *A. collinsii*, Ermentrout et al. (2003) hypothesized that *C. brevispinosa* should occur more often in late successional sites where acacias may be less healthy or in various stages of dying. However, they found that *C. brevispinosa* was absent from the acacias they sampled in a later successional site, but represented a relatively high proportion (32%) of the ant species on both large and small acacias in an early successional site. A possible explanation for this finding is that *C. brevispinosa* is a good colonizer of young *A. collinsii* but is either a poor defender of acacias or is outcompeted by other acacia ant species before the forest matures. We thus hypothesized that acacia ant species differ in their colonizing abilities, predicting that *C. brevispinosa* would occur more frequently on young acacias than would other acacia ant species. We also hypothesized that acacia ant species would not be equally effective defenders of their host acacias. We tested the specific prediction that *C. brevispinosa* colonies would be poor defenders of their host acacias when compared to the other two common species of acacia ants.

METHODS

On 10 January 2004 from 0830 to 1130, we studied the ant-acacia system in Palo Verde National Park, Guanacaste Province, Costa Rica. Our study site was located 6 km from the OTS field station (4 km on the road from the station

Table 1. Frequency of occurrence (%) of the most common ant species occupying young *A. collinsii* (≤ 1 m tall) and on all *A. collinsii* in the study plot (from Ermentrout et al. 2003).

	C. brevispinosa	*P. flavicornis*	*P. spinicola*	Total colonies
Young acacia	30.8	9.6	59.6	52
All acacia*	32.4	40.5	27.0	37

*Calculated from raw data of Ermentrout et al. (2003). Data are the frequencies of the most common ant species on isolated acacias and on the largest acacias > 1 m tall within clusters occupied by unique ant species.

and 2 km on La Carreta road; GPS location 16P 068 5939, 1147437). It consisted of second growth vegetation, including many acacias approximately 4-6 m tall. The site was burned in 1994 - 1995 and was currently being grazed by cattle.

To determine which ant species colonize young acacias, we surveyed ant populations on acacias ≤ 1 m tall in areas surrounding the permanent transects established by Ermentrout et al. (2003). We surveyed trees located 1 m or more from large (> 5 cm in diameter) acacias. Fifty two sample trees were tagged, their ant species were identified, and the health of each tree assessed using a 0 - 2 scale (0 = dead or sparse foliage, 1 = widely scattered foliage, and 2 = dense, lush foliage). We used G-tests to evaluate the null hypothesis that (1) ant species occurred with the same relative abundance on young plants as in the tree population as a whole, and (2) ant species occurred at random with respect to tree health.

To assess the defensive response behavior of the ant species, we selected nine healthy acacia trees (2 - 5 m in height) occupied by each of the three ant species (total of 27 trees). On each tree, we counted the number of ants passing an imaginary line on a large horizontal branch for 10 s before disturbance and considered this the baseline rate of ant activity. After applying a series of ten rapid taps at the line, we counted the number of ants crossing the line in three 10 s intervals separated by 5 s each. The three post-disturbance counts were very similar so were averaged to yield one measure per tree of pre- and post-disturbance activity (ants / 10 s). We employed a one-way ANOVA (of log transformed counts) to compare ant species with respect to pre-disturbance and post-disturbance ant activity. We used regression analyses to test the null hypothesis that species were the same in the relationship between pre- and post-disturbance activity (i.e., same slopes and intercept; Zar 1999).

Results

P. spinicola occupied 59.6% of the small acacia trees (≤ 1 m tall), followed by *C. brevispinosa* (30.8%) and *P. flavicornis* (9.6%) (Table 1). These relative abundances of ant species on young acacias (≤ 1 m tall) differed significantly from equal frequencies ($G = 21.05$, $df = 2$, $P < 0.0001$) and from those reported by Ermentrout et al. (2003) for trees in the same site ($G = 32.74$, $df = 2$, $P < 0.0001$; Table 1). On young trees in 2004, compared to all trees in 2003, *P. spinicola* abundance was higher, *C. brevispinosa* abundance was similar, and *P. flavicornis* abundance was much lower (Table 1).

The distribution of ant species on small acacias was related to the apparent health of trees ($G = 10.57$, $df = 4,46$ $P = 0.03$). *C. brevispinosa* occurred relatively more than *P. spinicola* or *P. flavicornis* on acacias with sparse, mostly dead foliage (health = 0) and relatively less on lush, densely foliated trees (health = 2), while *P. spinicola* occurred with relatively high

frequency on trees with lush foliage (health = 2) (Fig. 1).

There was no difference between ant species in their activity prior to disturbance (back-transformed means = 1.8 vs. 1.3 vs. 2.1 ants / 10 s for *C. brevispinosa*, *P. spinicola*, *P. flavicornis* respectively; $F_{2,24} = 0.41$, $P = 0.67$). All three species increased activity following disturbance, but there was no difference between species in post-disturbance activity (7.0 vs. 11.0 vs. 15.0 ants / 10 s; $F_{2,24} = 1.82$, $P = 0.18$). There was also no difference in the relationship between pre-disturbance and post-disturbance activity (Fig. 2).

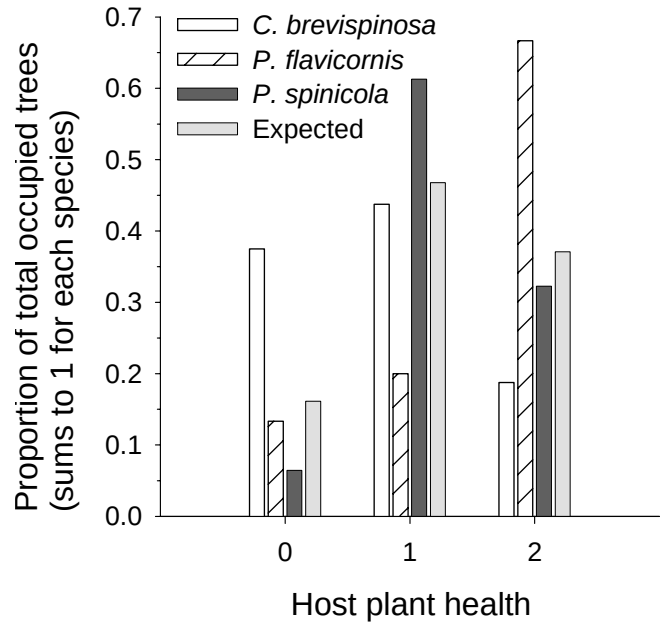

Figure 1. Frequency of ant species occupying acacia plants < 1 m tall of different health status (0 = foliage mostly dead/ very sparse (N = 10), 1 = foliage widely scattered/not dense (N = 29), 2 = foliage dense/lush (N = 23)). Expected values are based on the frequency of acacias in the three health categories.

DISCUSSION

According to our hypothesis that *C. brevispinosa* was the better colonizer of small acacias, we predicted that *C. brevispinosa* would be the most abundant species on young acacias ≤ 1 m tall. Instead, we found that *P. spinicola* was the most abundant, suggesting that *P. spinicola* is in fact the better colonizer in this early successional dry tropical forest site. However, *C. brevispinosa* did occupy 31% of the young acacias sampled, a relatively high percentage. Among these young acacias, *C. brevispinosa* occurred more often on unhealthy trees (health = 0), in accordance with Janzen's (1983) observations. The fact that many small and presumably young acacias were classified as unhealthy (health = 0) was unexpected, but this could account in part for the relatively high percentage of *C. brevispinosa* in our sample. Some *C. brevispinosa* were also found inhabiting healthy acacias (e.g. with health scores of 1 or 2). Therefore it is still unclear why *C. brevispinosa* occurred at such high frequency in both this year's sample of young trees and Ermentrout's transect samples of all trees in this early successional site. This requires future study.

The supposed symbiotic relationship be-

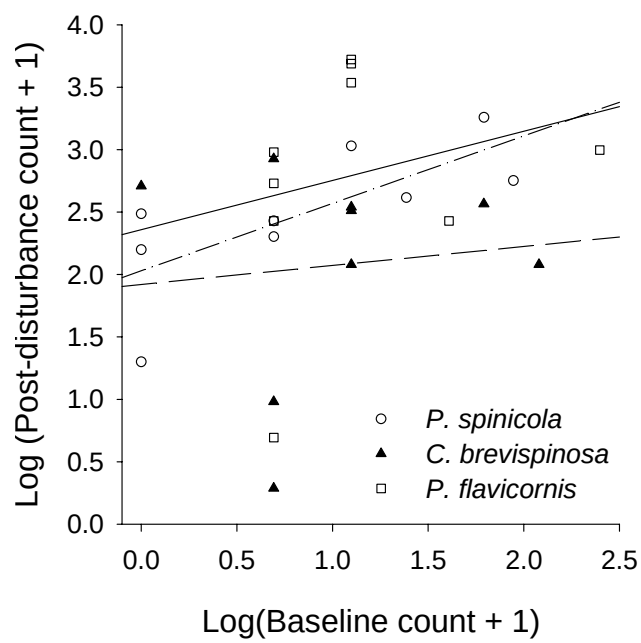

Figure 2. Comparison of ant species in their response to disturbance. In all species, activity was increased following disturbance, but there was no difference among species in the relationship between activity before and after disturbance. Best-fit regression lines are shown for each species separately (dash-dot line = *P. spinicola*; dashed line = *C. brevispinosa*; solid line = *P. flavicornis*), but regressions did not differ among species ($F2, 24 = 2.19$, $P > 0.10$).

tween *A. collinsii* and *C. brevispinosa* is also unclear. Although species differences were nonsignificant, *C. brevispinosa* was the least responsive to disturbance (Fig. 2), in accordance with our prediction that *C. brevispinosa* is a poor defender. It is unclear how much benefit acacia trees receive from *C. brevispinosa*, an ant species that may colonize dying trees and has a low defensive response to disturbance of its host tree.

An alternative hypothesis that we did not directly test is that *C. brevispinosa* may be outcompeted by other ant species as a forest matures. This would help explain why Ermentrout et al. (2003) found the species absent in their late successional forest site. Our measurement of aggressive response was not a measure of competitive ability, so we do not know the competitive ability of *C. brevispinosa* relative to other ant species. Further studies could use other methods, such as ant transplant experiments, to determine relative competitive abilities of acacia ant species, including *C. brevispinosa*.

Given that we tagged all the acacia trees in our sample, a future study could resample these trees in subsequent years to determine if there has been a change in tree health or the abundances of acacia ant species. More research is needed to explain the prevalence of *C. brevispinosa* at this early successional site and its potential symbiotic relationship with *A. collinsii*.

LITERATURE CITED

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