DIFFERENTIAL RESPONSE TO DISTURBANCE BETWEEN OBLIGATE AND FACULTATIVE ANT MUTUALISTS OF *ACACIA COLLINSII*

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Abstract: Due to their dependence on the host plant, obligate ant mutualists of the tree *Acacia collinsii* should defend their host more vigorously than facultative mutualists. We hypothesized that the activity level of the obligate mutualist *Pseudomyrmex spinicola* would respond more strongly to disturbance than that of the facultative mutualist *Crematogaster brevispinosa*. We also expected that ant response would depend on local resources provided by extra-floral nectaries. We found that *P. spinicola* did respond more vigorously to disturbance than *C. brevispinosa.* However, the response was unrelated to local resources. This indicates that, even though *P. spinicola* responds more strongly to disturbance of the host tree, the realized level of host defense may be similar for trees colonized by either ant mutualist.

Key Words: Crematogaster brevispinosa, *mutualism,* Pseudomyrmex spinicola

INTRODUCTION

Ant mutualists defend their host plant, which provides both habitat and energy resources (i.e. extra-floral nectaries; Janzen 1989). The activity level of obligate mutualists like the ant *Psuedomyrmex spinicola,* which can live only on *Acacia collinsii,* should respond strongly to disturbance. Increased activity level is likely to be associated with better defense of the host. In contrast, facultative mutualists, like the ant *Crematogaster brevispinosa,* may not exhibit the same strong response in activity levels. Ant response to disturbance may also depend upon the availability of resources provided by the host tree. Arnold et al. (2000) found that branches with experimentally reduced numbers of extra-floral nectaries had lower *P. spinicola* abundances, both before and after artificial disturbance. We predicted that the activity level of an obligate mutualist would exhibit a stronger response to disturbance than that of a facultative mutualist, and that local resource availability would be positively related to ant response for both types of mutualists.

METHODS

We haphazardly sampled 14 *A. collinsii* trees of approximately equal height (to control for effects of tree size) at a site near the main road, 2 km east of the OTS biological station at Palo Verde National Park, Costa Rica. We chose seven trees colonized by *P. spinicola* and seven colonized by *C. brevispinosa*. To control for effects of tree size, we chose trees of approximately equal height.

We quantified the number of leaves, nectaries, total thorns, occupied thorns, and length of woody tissue on one branch

per tree. We selected branches with varying numbers of leaves and thorns, so that we could evaluate ant responses across a range of resource abundances.

We chose a point on each selected branch and counted the number of ant crossings ("ant activity") at that point over five-minute periods, prior to and following the disturbance. The disturbance consisted of vigorous tapping for 10 s at the beginning of each minute interval.

Data were analyzed with one-way ANOVA and linear regression tests using JMP version 5.0.1.

RESULTS

Pre- and post-disturbance number of ant crossings were normalized by logarithmic transformation. Pre-disturbance ant activity was positively related to post-disturbance ant activity in *C. brevispinosa* ($r^2 = 0.97$, df = 1, 5, $P < 0.0001$), but not in *P. spinicola* ($r^2 = 0.02$, df = 1, 5, $P = 0.74$; Fig. 1).

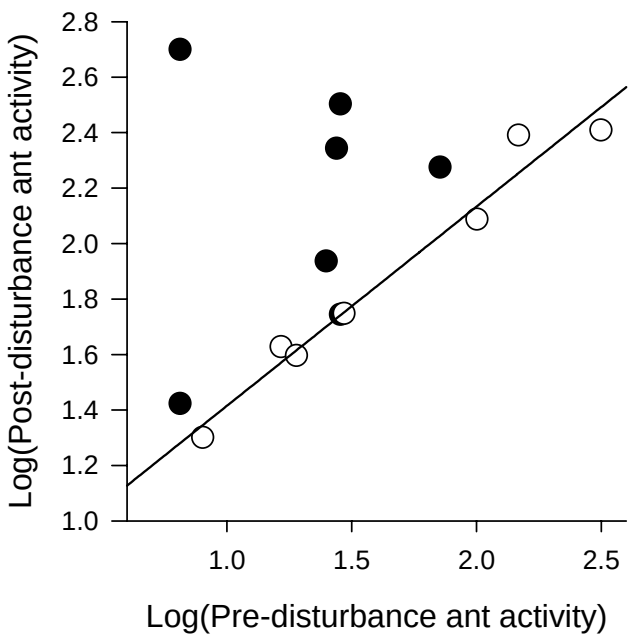

Figure 1. *Pseudomyrmex spinicola* and *Crematogaster brevispinosa* activity before and after disturbance. Filled circles represent *P. spinicola* and open circles *C. brevispinosa*. Line is a least-squares linear regression.

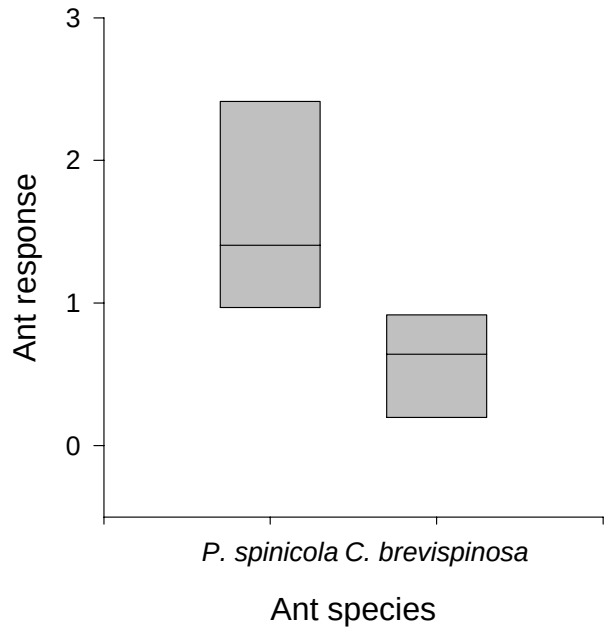

Figure 2. Response to disturbance of *Acacia collinsii* by the obligate ant mutualist *Pseudomyrmex spinicola* (n = 7) and facultative mutualist *Crematogaster brevispinosa* (n = 7). To calculate ant response, we divided the number of ants crossing a line on a branch for five minutes prior to artificial disturbance, by the number of ants crossing that line for five minutes following the artificial disturbance. The disturbance consisted of vigorous tapping.

We divided post- by pre-disturbance numbers of ant crossings, to obtain an index of change in ant activity, which will hereafter be referred to as ant response to disturbance. *P. spinicola* responded more strongly to disturbance than *C. brevispinosa* ($t = -2.70$, df = 12, $P = 0.02$; Fig. 2).

We found no relationship between ant response to disturbance and number of nectaries per unit branch length, for either *P. spinicola* or *C. brevispinosa*. Neither was there any relationship between ant re-

Table 1. Results of linear regressions of *Pseudomyrmex spinicola* and *Crematogaster brevispinosa* response on several measures of resource availability on *Acacia collinsii* branches. To calculate ant response, we divided the number of ants crossing a line on a branch for five minutes prior to artificial disturbance, by the number of ants crossing that line for five minutes following the artificial disturbance. The disturbance consisted of vigorous tapping.

Source	r^2	df	F	P
Number of nectaries / cm branch				
P. spinicola	0.05	1, 5	0.27	0.10
C. brevispinosa	0.03	1, 5	0.18	0.69
Length of branch	0.00	1, 12	0.04	0.84
Number of occupied thorns	0.16	1, 12	2.22	0.16
Number of leaves	0.02	1, 12	0.22	0.64

sponse and length of branches, number of occupied thorns, or number of leaves (Table 1).

We also compared post-disturbance ant activity of the two ant species, to determine the relative intensity of defense each provides to the host tree; we found no difference between the two species (F = 1.16, df = 1, 12, P = 0.30).

DISCUSSION

The obligate mutualist *P. spinicola* responded more vigourously to artificial disturbances than the facultative *C. brevispinosa*. *Pseudomyrmex spinicola* maintained a relatively low baseline level of activity, but exhibited a high post-disturbance activity level relative to that baseline. In contrast, the facultative *C. brevispinosa* did not respond to disturbance. Its pre- and post-disturbance activity were similar to *P. spinicola's* post-disturbance activity. These results are supported by Wickre et al. (2003), who observed a higher patrol rate in *C. brevispinosa* than in *P. spinicola*. This indicates that the two species may provide equivalent levels of defense to their host plants, even though *P. spinicola* responds more vigorously to disturbance.

The absence of positive relationships between resources (i.e. nectaries, thorns and leaves), and ant response to disturbance is consistent with the observations of Arnold et al. (2000), who found no relation between the presence of nectaries and ant abundance. For mutualist ants, the fate of the colony may be tied to the survival of the entire tree, rather than depending on the defense of resource-rich branches. Even though *P. spinicola* responds more strongly to disturbance of the host tree, the realized level of host defense may be similar for trees colonized by either ant mutualist. This interpretation rests upon the assumption that individuals of each species are equivalent in their ability to deter herbivores (i.e., severity or rate of bites from each species are equivalent). Future studies could test the validity of this assumption by examining the attack rate or efficacy of herbivore deterrence for each ant species.

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EFFECT OF COLOR AND SIZE ON AGGRESSIVE BEHAVIOR AND FEMALE ACCESS IN THE LIZARD *CTENOSAURA SIMILIS*

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Abstract: Male *Ctenosaura similis* are highly territorial lizards that vary greatly in their physical attributes. We studied the effects of mature male size and color on territorial head-bobbing displays and access to females in Palo Verde National Park, Costa Rica. We hypothesized that large orange males would show more frequent head-bobbing behavior, and have more females in their territories, than smaller or blue-colored individuals. Orange males did have more females in their territories, but we were unable to separate the effects of male color and size on number of females. Neither size nor color influenced head-bobbing behavior.

Key Words: head-bobbing, male coloration, sexual selection, territoriality

INTRODUCTION

Ctenosaura similis, a large Central American iguanid lizard, exhibits both color-change and head-bobbing behavior. Coloration and body size vary among mature individuals. Within individuals color may vary both seasonally and daily, and also with developmental stage (Fitch and Hackforth-Jones 1983). During the breeding season, some adults, which normally range from tan to gray-blue in color, may develop spots of dull red or orange coloration, although little is known about the function of this coloration (Fitch and Hackforth-Jones 1983).

Ctenosaura similis uses head-bobbing displays to communicate with conspecifics (Fitch and Hackforth-Jones 1983). Vanderbuilt et al. (1990) described two distinct bobbing behaviors of males, one for territorial displays and another for courtship of