

———. 1979. Co-evolution of figs and their insect pollinators. *Annu. Rev. Ecol. Syst.* 10: 1–12.

### Aviva Patel<sup>2</sup>

Department of Biology  
University of Miami  
Coral Gables, Florida 33124, U.S.A.

<sup>2</sup> Current address: Ecosystem Health, Blackwood Hall, University of Guelph, Guelph, Ontario, Canada N1G 2W1; email: avivapat@uoguelph.ca

BIOTROPICA 30(3): 480–482 1998

## Defense of *Acacia collinsii* by an Obligate and Nonobligate Ant Species: the Significance of Encroaching Vegetation<sup>1</sup>

*Key words:* *Acacia*; ants; *Costa Rica*; *Crematogaster*; herbivory; mutualism; *Pseudomyrmex*.

THOMAS BELT (1874) WAS THE FIRST TO DESCRIBE the association between *Acacia* trees and *Pseudomyrmex* ants. Belt hypothesized that a mutualism existed between ant and plant in which acacias supplied food (in the form of extrafloral nectaries and Beltian bodies) and shelter (hollowed-out thorns) for the ants while the ants in turn protected the tree from herbivory and encroaching vegetation. Janzen (1966) tested this hypothesis experimentally and showed that herbivory drastically increased on *Acacia* trees whose ants had been removed. Other studies have also supported the hypothesis of a mutualistic relationship between *Acacia* and *Pseudomyrmex* ants based on protection from herbivory (Brown 1960, Janzen 1967a, 1973; Holldobler & Wilson 1990). However, the selective advantage of clearing vegetation around the host *Acacia* is still unclear. The ants may be trying to reduce competition between the host plant and other vegetation (Janzen 1967b) or they may be preventing invasion or confrontation from other ant colonies through contact with a tree inhabited by a different species (Davidson *et al.* 1988).

In the Guanacaste Province of Costa Rica, three species of *Pseudomyrmex* ants commonly inhabit *Acacia collinsii*: *Pseudomyrmex flavicornis* (= *P. belti*), *P. spinicola*, and *P. nigrocinctus* (Janzen 1985, Ward 1993). A fourth species of ant, *Crematogaster brevispinosa*, also inhabits *A. collinsii*. However, it is unknown if the relationship is mutualistic or if *C. brevispinosa* is exploiting the resources provided by the tree without providing a benefit in return. While the three *Pseudomyrmex* species are obligate *Acacia* ants (Ward 1993), *C. brevispinosa* typically inhabits tree hollows, logs, and dead *Acacia* trees (Gill, pers. comm.). For those *Crematogaster* ants that inhabit apparently healthy acacias, it is unknown whether the tree was colonized after it was abandoned by *Pseudomyrmex* ants or if *C. brevispinosa* can competitively displace *Pseudomyrmex* colonies.

We examined the role of encroaching vegetation on the aggressive interactions between two species of ants, *Pseudomyrmex spinicola* and *Crematogaster brevispinosa*, and the ability of these two species of ants to protect *Acacia collinsii* from herbivory. We expected the obligate inhabitant, *P. spinicola*, to be a better mutualist with *A. collinsii* than the generalist *C. brevispinosa*. Since *C. brevispinosa* are not dependent on acacias for nest sites, they should not invest as much time or resources protecting the plant from herbivory or encroaching vegetation. Alternatively, *P. spinicola* should defend the acacia more rigorously, particularly if nest sites are limited. Specifically, we predicted that: obligate *P. spinicola* would provide acacias with better protection against herbivory than would the generalist *C. brevispinosa*; *P. spinicola* would be more aggressive toward intruders than *C. brevispinosa*; and *P. spinicola* would prevail in forced interactions between the two ant species.

The study was conducted on 26–30 January 1994, at Playa Naranjo in Santa Rosa National Park, Guanacaste Province, Costa Rica. All measurements were taken in a 1-ha plot of tropical dry forest along the Sendero Aceituna trail. *Acacia collinsii* is the most common understory tree in the study plot.

To compare the abilities of *P. spinicola* and *C. brevispinosa* to defend *A. collinsii* from herbivory, ten trees inhabited only by *P. spinicola* were paired with ten similarly sized trees containing only *C. brevispinosa*. The

<sup>1</sup> Received 27 August 1996; revision accepted 20 May 1997.

2 terminal and 2 innermost leaves were taken from the highest, lowest and 3 randomly chosen branches for a total of 20 leaves from each tree. Each leaf was then scored from 1–5 based on a percentage of herbivore damage found on the leaf (1 = 0–12.5%; 2 = 12.5–25%; 3 = 25–50%; 4 = 51–75%; 5 = 76–100%). This included any modification to the leaf that was clearly caused by an herbivore. An unpaired *t*-test was used to compare mean herbivore damage on trees inhabited by the two ant species. A comparison to trees that lacked any ant inhabitants could not be done because all trees in our plot were occupied at the time of the study.

To quantify aggression toward a potential herbivore, we secured equal-sized katydids to a pair of trees, one containing *Pseudomyrmex spinicola* and the other *Crematogaster brevispinosa*. The katydids were fastened with string to the trunk of the tree approximately 1.5 m off the ground. The number of ants attacking the katydids were then recorded each minute for 10 min, then every 5 min for the next 20 min.

To measure aggressive interactions between the two ant species, branches from two pairs of adjacent trees, one containing *P. spinicola* and the other *C. brevispinosa*, were secured together with 1 in diameter tape 1.5 m off the ground. The paired trees were of similar height and less than 2 m away from each other. The secured branches were marked at 10 cm intervals from the middle of the connection towards each trunk. The amount of fighting and distance encroached by each ant species was recorded every 4 h over the next 3 d.

The obligate mutualist *Pseudomyrmex spinicola* may defend *Acacia collinsii* against herbivores more effectively than the generalist *Crematogaster brevispinosa*. Leaf herbivory averaged 12 percent lower in acacias containing *P. spinicola*, although the difference was not statistically significant (mean herbivory score  $\pm$  SE: *P. spinicola* = 1.784  $\pm$  0.118; *C. brevispinosa* = 1.949  $\pm$  0.122; *t*-test, *df* = 18, *t* = 0.973, *P* = 0.17). There was one conspicuous outlier (>2 SD above the *x*). We omitted this outlier and obtained a significant difference (mean herbivory score  $\pm$  SE: *P. spinicola* = 1.693  $\pm$  0.084; *C. brevispinosa* = 1.949  $\pm$  0.122; *t*-test, *df* = 17, *t* = 1.687, *P* = 0.05).

*Pseudomyrmex spinicola* was more aggressive to the katydid on their host tree than *Crematogaster brevispinosa*. While there were never more than 2 workers of *C. brevispinosa* attacking the katydid at any one time throughout the 30 min trial 15 *P. spinicola* workers were attacking the katydid within 5 min. Throughout the remaining 25 min, a *x* of 19.7  $\pm$  3.4 ( $\pm$  SD) *P. spinicola* workers were attacking the katydid at any 5 min interval. Strong conclusions cannot be drawn from this experiment, however, because it was not replicated and the results may be a function of a particularly unaggressive *C. brevispinosa* colony. *Crematogaster brevispinosa* appears to be benefiting from the acacia while providing less defense against herbivory than *P. spinicola*. However, we cannot exclude the possibility that *Crematogaster* ants are taking over trees that have already been badly damaged by herbivores.

In trees artificially connected by tape, both ant species within each trial initially made very slight advances across the midpoint. Shortly thereafter, fighting ensued between the species. The battlefront was spread out linearly over 6 cm, centered at the midpoint of the connected branches. After intense fighting that continued steadily for the first day, a small (7 cm) gain was established by *Crematogaster brevispinosa* in both pairs of trees. After three days, *C. brevispinosa* maintained a 12 cm gain in one of the pairs and had completely taken over the tree occupied by *P. spinicola* in the other.

Our observations of interspecific interactions between *Pseudomyrmex spinicola* and *Crematogaster brevispinosa*, suggest that *C. brevispinosa* may invade trees occupied by *P. spinicola*. We also observed *C. brevispinosa* taking over a tree occupied by *Pseudomyrmex nigrocincta* in a similar forced-encounter experiment. Further investigation revealed dead *P. nigrocincta* inside of the thorns on two other *Acacia* trees inhabited by *C. brevispinosa* within our plot, suggesting that *C. brevispinosa* had overtaken these trees (although not necessarily when *P. nigrocincta* was alive). If *C. brevispinosa* can take over *Pseudomyrmex* trees, we would expect to see *Pseudomyrmex* ants displaced by *Crematogaster* within our plot, but this does not seem to be occurring over a large scale. Why the displacement of *Pseudomyrmex*-occupied trees by *C. brevispinosa* is not more common is unclear. Perhaps *C. brevispinosa* is only capable of invading degraded *Pseudomyrmex* colonies or perhaps forced interactions (*i.e.*, through the contact of encroaching vegetation) are necessary for an invasion to take place. In a similar study on the plant *Triplaris americana* in Peru, aggressive interactions between *Pseudomyrmex* and *Crematogaster* ants increased when artificial bridges were secured between plants (Davidson *et al.* 1988). These findings suggest that the function of pruning alien vegetation by *Pseudomyrmex* is to prevent bridgeheads being established that would permit invasion by alien ants.

More studies are needed comparing interactions between *Crematogaster brevispinosa* and other *Pseudomyrmex* species. To examine the possibility that *Crematogaster* ants are colonizing heavily damaged or dying trees, the amount of herbivory over time should be quantified. Future studies should examine tree occupancy by *C. brevispinosa* and how this changes over time. Specifically, are trees previously inhabited by *Pseudomyrmex* being invaded by *C. brevispinosa*, or does *C. brevispinosa* simply colonize trees abandoned by *Pseudomyrmex*?

This project was made possible through generous support from the Organization for Tropical Studies. We would also like to thank Bruce Young, Doug Futuyma, Phil Ward and Ted Case for helpful comments on the manuscript.

BELT, T. 1874. *The naturalist in Nicaragua*. John Murray, London, England.

BROWN, W. L. 1960. Ants, acacias, and browsing mammals. *Ecology* 41: 587–592.

DAVIDSON, D. W., J. T. LONGINO, AND R. R. SNELLING. 1988. Pruning of host plant neighbors by ants: an experimental approach. *Ecology* 69: 801–808.

HOLLDOBLE, B., AND E. O. WILSON. 1990. *The Ants*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

JANZEN, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution* 20: 249–275.

———. 1967a. Interaction of the bull's-dash horn acacia (*Acacia cornigera*) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. *University of Kansas Science Bulletin* 47: 315–558.

———. 1967b. Fire, vegetation structure, and the ant x acacia interaction in Central America. *Ecology* 48: 26–35.

———. 1973. Evolution of polygynous obligate acacia-ants in western Mexico. *J. Anim. Ecol.* 42: 727–750.

———. 1985. *Pseudomyrmex ferruginea*. In D.H.Janzen (Ed.). *Costa Rican natural history*, pp. 762–764. University of Chicago Press, Chicago, Illinois.

WARD, P. S. 1993. Systematic studies on *Pseudomyrmex* acacia-ants. *J. Hymenoptera Res.* 2: 117–168.

#### Andrew V. Suarez<sup>2</sup>

Department of Ecology  
Ethology and Evolution  
University of Illinois  
Urbana, Illinois 61801, U.S.A.

#### Consuelo De Moraes

Department of Entomology  
University of Georgia  
Athens, Georgia 30602, U.S.A.

and

#### Anthony Ippolito

Division of Biological Sciences  
University of Missouri  
Columbia, Missouri 65211, U.S.A.

---

<sup>2</sup> Current address: Department of Biology 0116, University of California at San Diego, La Jolla, California 92093, U.S.A. (Corresponding author).

## Parasitic Phorid Flies (Diptera: Phoridae) Associated with Army Ants (Hymenoptera: Formicidae: Ecitoninae, Dorylinae) and their Conservation Biology<sup>1</sup>

*Key words:* parasitoids; hosts; natural history.

The most abundant insects living as guests or myrmecophiles within colonies of army ants are tiny flies of the family Phoridae (Rettenmeyer & Akre 1968).

---

<sup>1</sup> Received 15 November 1996; revision accepted 25 March 1997.