

SHORT COMMUNICATION

Facultative ant association benefits a Neotropical orchid

BRIAN L. FISHER

Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA

KEY WORDS: ants, ant-plant interactions, *Caularthron*, mutualism, Orchidaceae, Panamá.

Epiphytic plants have evolved a diverse array of associations with ants that promote the provisioning of moisture, nutrients, or physical protection (Davidson & Epstein 1989). Ant-epiphyte associations are often based on: (1) the occasional use of carton (= paper) nests constructed by ants as substrate for establishment and growth of epiphytes (Longino 1986); (2) the production of extrafloral nectar by epiphytes to attract opportunistic ant 'guards' (Bentley 1977, Fisher & Zimmerman 1988); (3) the production of 'domatia' or hollow cavities in epiphytes that house ant associates (Benzing 1970, Huxley 1978); or (4) the seed dispersal of epiphytes by ants, which create 'ant-gardens' (Davidson 1988). These associations are not exclusive; they can be found in combination and may result from opportunistic or obligate interactions between ants and epiphytes.

In epiphytic orchids, extrafloral nectaries are the most common structures that give rise to associations with ants (Fisher & Zimmerman 1988). Extrafloral nectaries may be effective in providing a facultative means of defence because arboreal ants are the most common group of insects in the tropical forest canopy (Benson 1985, Erwin 1983, Wilson 1987). A few orchid species have been reported to occur only on ant nests (e.g. *Coryanthes*, *Epidendrum imatophyllum* Lindl.) but no detailed studies have investigated these associations (Dressler 1981). Two genera of orchids (*Caularthron* and *Schomburgkia* section *Chauno-Schomburgkia*) are known to provide nesting sites for ants in hollow pseudobulbs (Dressler 1981, Fisher & Zimmerman 1988, Kennedy 1979, Rico-Gray *et al.* 1989).

Although a few studies have demonstrated positive effects of obligate, symbiotic ant associates on host plants (Janzen 1972, Schupp 1986), the effect of facultative, symbiotic ants on host plants has received less attention (Beattie 1985, Rico-Gray 1987). This investigation experimentally evaluates the effect of facultative ant occupants on the production of reproductive structures in an epiphytic orchid, *Caularthron bilamellatum* (Rchgf.) Schult., in Panama.

The study was conducted during the dry season of 1987 at the Smithsonian

Tropical Research Institute facilities within the Barro Colorado Nature Monument. The Nature Monument is a protected area of lowland, semi-deciduous tropical forest with an annual rainfall averaging 2600 mm and a four month dry season between December and April (Croat 1978, Leigh *et al.* 1982).

Pseudobulbs of *C. bilamellatum* are filled with a parenchymous tissue that lacks major vascular bundles and desiccates at the onset of the dry season, forming a hollow chamber. Queen ants then enter the pseudobulbs through preformed basal slits and use the chambers as nest sites. Ant frass and discarded parts of prey are deposited in the apical end of the hollow pseudobulbs. Unlike rubiaceaceous myrmecophytes (Huxley 1978, Rickson 1979), the inner tissues of the hollow pseudobulbs do not exhibit any specialized tissue for absorption of ant deposited nutrients (F. Rickson, pers. comm.), although roots of *C. bilamellatum* are occasionally observed inside hollow pseudobulbs with ant frass deposits.

Extrafloral nectaries are located at the base of the leaves, and on the peduncles, pedicels, buds and fruits (Fisher & Zimmerman 1988, Fisher *et al.* 1990). *C. bilamellatum* is the only orchid documented to produce extrafloral nectar on vegetative structures (Fisher & Zimmerman 1988), and therefore is the only orchid known to produce extrafloral nectar throughout the year. Preliminary extrafloral nectar sugar analyses of four *C. bilamellatum* orchids revealed on average 47% sucrose, 23% glucose, and 30% fructose (I. Baker, pers. comm.).

During the study, ants were observed foraging on extrafloral nectar both during the day and night but were more common at night. In a survey within the Nature Monument, 11 species of ants were observed nesting with queens in pseudobulbs of *C. bilamellatum* (Fisher & Zimmerman 1988). These 11 ant species are not obligate associates but are common canopy ants. A random sample of common host trees of *C. bilamellatum* that were without the orchid showed the same frequencies of ant species that inhabit *C. bilamellatum*, indicating that the interactions are non-specialized and facultative, rather than obligate (Fisher & Zimmerman 1988).

To determine the effects of ants on bud, flower and fruit production of *C. bilamellatum*, I compared orchids with and without ants and ant refuse. Ants and ant refuse were forced out of the basal slit of occupied pseudobulbs by using a portable air pump. The basal slits were then sealed and a ring was smeared around the branch with Tanglefoot (The Tanglefoot Company, Grand Rapids, Michigan, USA) to prevent ants from re-entering the orchids. As the effect of ants might vary with the size of the plant, I examined orchids in two size categories: (1) orchids with five pseudobulbs, and (2) orchids with 10 pseudobulbs.

Around the margins of Gatun Lake, I located 20 pairs of *Annona glabra* L., Sp. trees, growing between 1 and 10 m apart, that had both small and large orchids growing on them. In early November 1986, two months before the reproductive season of the orchid, trees were designated in an alternating fashion, as either control (ants and refuse present) or experimental (ants and refuse removed). Because of the difficulty in finding trees with both 5 and 10 pseudobulb orchids, the experimental design included: (1) 19 small and 13 large orchids with ants;

and (2) 20 small and 16 large orchids with ants removed. In the ant present treatment, *Azteca velox* Forel (Dolichoderinae) occupied 15 small orchids and 12 large orchids, *Paratrechina pubens* Forel (Formicinae) occupied 4 small orchids and 1 large orchid, and *Hypoclinea bispinosa* Forel (Dolichoderinae) occupied 1 small orchid.

The total number of buds, flowers and fruits on all inflorescences of each plant was censused weekly for 16 weeks from 14 January to 30 April 1987 during the reproductive phase of the orchid.

The overall design followed a randomized block analysis of variance (ANOVA), with blocks as the site of paired trees and factorials as ants and size treatments. The effects of ants on reproductive parameters was determined by analyses of variance (SAS 1987) on values which were square root transformed to normalize distributions.

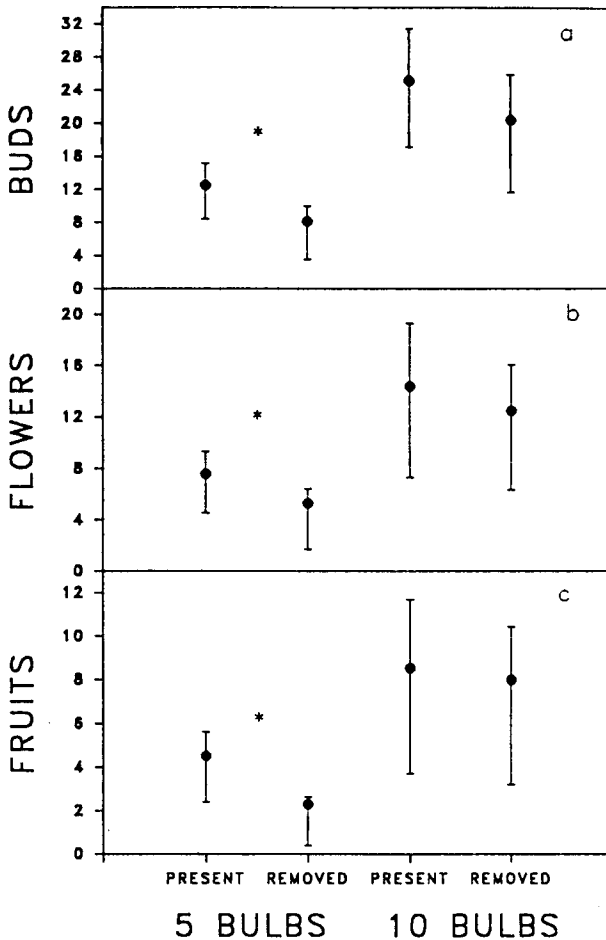


Figure 1. The effects of ants on reproductive parameters of *C. bilamellatum*. Back-transformed means and 95% confidence intervals of: (a) buds, (b) flowers, and (c) fruits produced by small (5 pseudobulbs) and larger (10 pseudobulbs) *Caularthron bilamellatum* orchids. Sample sizes include 19 small and 13 larger orchids with ants present, and 20 small and 16 larger orchids with ants removed. * indicates a significant difference in means (*a posteriori* analyses, $P < 0.05$, one-sided test).

herbivores; or (2) nutrients or moisture from ant nests inside hollow pseudobulbs. Although information on anti-herbivore protection and nutrient absorption was not collected in this study, studies on *Schomburgkia tibicinis* Batem., which has similar anatomy to *Caularthron*, support both hypotheses; *S. tibicinis* absorbed labelled carbon from dead insects deposited inside the hollow pseudobulbs and some ant occupants were effective in disrupting the feeding activity of herbivorous beetles (Rico-Gray 1987, Rico-Gray *et al.* 1989). But as cautioned by Horvitz & Schemske (1984), the experimental evaluation of the effect of ant associates requires testing at a variety of sites and times. The effect of ant occupants on orchid fitness may alter with a change in herbivore pressure, environmental stress, or orchid substrate and, as shown in this study, with plant size.

A complimentary study (Fisher *et al.* 1990) demonstrated that ant occupants of *C. bilamellatum* benefit, in varying degrees, from extrafloral nectar consumption. At this stage, we do not know whether ant species differ in their effects on orchid fitness (Rico-Gray 1987), or whether there is selection for host plant specialization by a single ant species or a suite of ant species.

Acknowledgements. I thank M. Aide, D. Davidson, D. Feener, A. Herre, H. Howe, M. Keller, G. Schupp, and J. Zimmerman for assistance during various stages of the project, R. Snelling for ant identification, I. Baker for extrafloral sugar analyses, F. Rickson for assistance in anatomical studies, and the Editor and an anonymous reviewer for critical comments on the manuscript. The project was supported by NSF grant BSR-8604687 to H. Howe. I also thank the Smithsonian Tropical Research Institute for logistic assistance and the use of their facilities. Manuscript preparation was supported by the University of Utah.

LITERATURE CITED

- BEATTIE, A. J. 1985. *The evolutionary ecology of ant-plant interactions*. Cambridge University Press, Cambridge.
- BENSON, W. 1985. *Amazonian ant-plants*. Pp. 239–266 in Prance, G. & Lovejoy, T. (eds). *Amazonia*. Pergamon, Oxford.
- BENTLEY, B. 1977. Extrafloral nectaries and protection by pugnacious bodyguards. *Annual Review of Ecology and Systematics* 8:407–427.
- BENZING, D. H. 1970. An investigation of two bromeliad myrmecophytes: *Tillandsia butzii* Mez., *T. caput-medusae*. E. Morren and their ants. *Bulletin of the Torrey Botanical Club* 97:109–115.
- CROAT, T. B. 1978. *The flora of Barro Colorado Island*. Stanford University Press, Stanford.
- DAVIDSON, D. W. 1988. Ecological studies of neotropical ant gardens. *Ecology* 69:138–1152.
- DAVIDSON, D. W. & EPSTEIN, W. W. 1989. Epiphytic associations with ants. Pp. 200–233 in Lüttge, U. (ed.). *Vascular plants as epiphytes*. Springer Verlag, Berlin.
- DRESSLER, R. L. 1981. *The orchids: natural history and classification*. Harvard University Press, Cambridge.
- ERWIN, T. L. 1983. Tropical forest canopies: the last biotic frontier. *Bulletin of the Entomological Society of America* 29:14–19.
- FISHER, B. L. & ZIMMERMAN, J. K. 1988. Ant/orchid associations in the Barro Colorado National Monument, Panama. *Lindleyana* 3:12–16.
- FISHER, B. L., STERNBERG, L. D. L. & PRICE, D. 1990. Variation in the use of extrafloral nectar by ants. *Oecologia* (Berl.) 83:263–266.
- HORVITZ, C. C. & SCHEMSKE, D. W. 1984. Effects of ant-mutualists and an ant-sequestering herbivore on seed production of a tropical herb *Calathea ovandensis* (Marantaceae). *Ecology* 65:1369–78.
- HUXLEY, C. R. 1978. The ant-plant *Myrmecodia* and *Hydnophytum* (Rubiaceae) and the relationships between their morphology, ant occupants, physiology and ecology. *New Phytologist* 80:231–268.
- JANZEN, D. H. 1972. Protection of *Barteria* (Passifloraceae) by *Pachysima* ants (Pseudomyrmecinae) in a Nigerian rain forest. *Ecology* 53:885–892.

- KENNEDY, G. C. 1979. The genus *Schomburgkia* and *Myrmecophilia*. *Orchid Digest* Nov/Dec:204–212.
- LEIGH, E. G., RAND, A.S. & WINDSOR, D.M. (eds). 1982. *The ecology of a tropical rain forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington.
- LONGINO, J. T. 1986. Ants provide substrate for epiphytes. *Selbyana* 9:100–103.
- RICKSON, F. R. 1979. Absorption of animal tissue breakdown products into a plant stem – the feeding of a plant by ants. *American Journal of Botany* 66:87–90.
- RICO-GRAY, V. 1987. *Schomburgkia tibicinis* Batem. (Orchidaceae) – effect of myrmecophyly on reproductive fitness. PhD dissertation, Tulane University, New Orleans.
- RICO-GRAY, V., BARBER, J. T., THIEN, L. B., ELLGAARD, E. G. & TONEY, J. J. 1989. An unusual animal-plant interaction: feeding of *Schomburgkia tibicinis* (Orchidaceae) by ants. *American Journal of Botany* 76:603–608.
- SAS. 1987. SAS/STAT guide for personal computers. (version 6 edition). SAS Institute, Cary, NC.
- SCHUPP, E. W. 1986. Azteca protection of *Cecropia*: ant occupation benefits juvenile trees. *Oecologia* (Berl.) 70:379–385.
- WILSON, E. O. 1987. The arboreal ant fauna of Peruvian Amazon forest: a first assessment. *Biotropica* 19: 245–251.

Accepted 20 February 1991

ANNOUNCEMENT

EcoCiencia – Ecuador

EcoCiencia, the Ecuadorian Foundation of Ecological Studies, is a private, non-profit organisation started in 1989. Its main activities are the support of scientific studies aimed at conservation and environmental education. It is currently developing an Environmental Documentation Centre which includes a library of almost 2000 books, 500 journals and magazines and 500 reprints, mainly in Spanish and English. There is also a collection of 1500 slides for use in education.

For further information contact:

Danilo Silva Chiriboga, MSc,

Executive Director, EcoCiencia, Av. 12 de Octubre 959 y Roca, Edificio Mariana de Jesús – Of. 701, PO Box 17-12-00257, Quito, Ecuador.