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SHORT COMMUNICATION

## Facultative ant association benefits a Neotropical orchid

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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 rubiaceous 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.

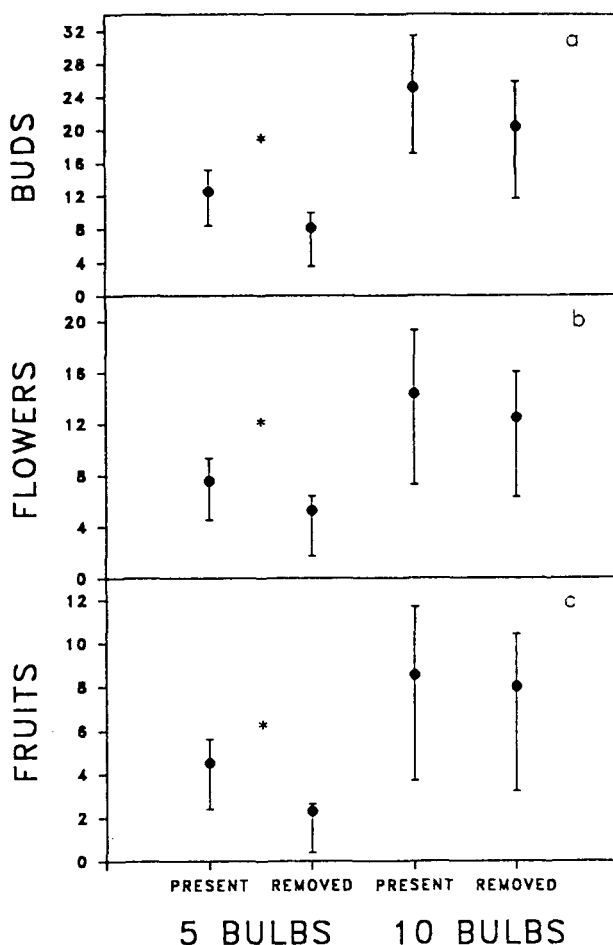


Figure 1. The effects of ants on reproductive parameters of *C. bilamellatum*. Back-transformed means and 95% confidence intervals of: (a) buds, (b) flowers, and (c) fruits produced by small (5 pseudobulbs) and larger (10 pseudobulbs) *Caularthron bilamellatum* orchids. Sample sizes include 19 small 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).

Table 1. Two-way analysis of variance results for number of buds, flowers, and fruits produced by *C. bilamellatum* as a function of site (paired trees), size (5 and 10 pseudobulbs), ant (present and removed) and interaction of ant treatment and size class. Dependent variables were analyzed with square root transformations.

Dependent Variable	Source	R <sup>2</sup>	df	MS	F	P
Bud	Size	0.32	1	37.91	25.58	< 0.001
	Ant		1	9.08	6.13	0.017
	Size × Ant		1	0.21	0.14	0.706
	Site		19	2.19		
	Error		45	1.48		
Flower	Size	0.21	1	16.60	14.04	0.001
	Ant		1	3.21	2.71	0.106
	Size × Ant		1	0.85	0.72	0.402
	Site		19	2.50		
	Error		45	1.18		
Fruit	Size	0.24	1	16.79	18.85	< 0.001
	Ant		1	4.43	4.98	0.031
	Size × Ant		1	1.70	1.91	0.174
	Site		19	2.03		
	Error		45	0.89		

Both small and large orchids occupied by ants produced a greater number of buds, flowers and fruits than did orchids with ants and ant refuse removed (Figure 1). Two way analysis of variance results demonstrate a significant main effect of size on number of buds, flowers and fruit (Table 1). The treatment effect of ants is significant only on number of buds and fruit produced, not flowers. For all dependent variables, there was no significant interaction between orchid size and the treatment effects of ants.

*A posteriori* analyses were used to test the null hypothesis that the presence of ants does not cause an increase in reproductive output for each size class of orchid. The null hypothesis could not be rejected for the 10 pseudobulb size class (Bud:  $F_{1,45} = 1.92$ ,  $P = 0.087$ ; Flower:  $F_{1,45} = 0.29$ ,  $P = 0.298$ ; Fruit:  $F_{1,45} = 0.33$ ,  $P = 0.285$ ), but was rejected for the 5 pseudobulb size class for bud, flowers and fruit production (Bud:  $F_{1,45} = 4.93$ ,  $P = 0.016$ ; Flower  $F_{1,45} = 3.74$ ,  $P = 0.030$ ; Fruit:  $F_{1,45} = 7.85$ ,  $P = 0.004$ ). Therefore, only small orchids produced a significantly greater number of reproductive structures in response to the presence of ants (Figure 1).

The results of this experiment suggest that the *C. bilamellatum*-ant interaction is mutualistic. Because only small orchids with ants produced significantly more buds and fruits, the magnitude of the beneficial effects of ants on plant associates must vary with age of host plants. The association with ants may also result in an increase in orchid fitness due to an early age of first reproduction. At the population level, the importance of this interaction can be inferred in part from the high frequency of the association. During the year of this study, Fisher & Zimmerman (1988) documented that 85% of the orchids ( $N = 573$ ) were occupied by ants.

*C. bilamellatum* may benefit from ant occupants because of: (1) protection from

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.

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