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ANT/ORCHID ASSOCIATIONS IN THE BARRO COLORADO NATIONAL MONUMENT, PANAMA[1]

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ABSTRACT

Of 23 orchid species studied at Barro Colorado National Monument in central Panama, 16 were found to produce extrafloral nectar. Extrafloral nectaries were found primarily on reproductive structures and developing shoots. Only one species (*Caularthron bilamellatum*) showed evidence of ant occupation, indicating that most orchids are not likely to derive nutritional benefit from their associations with ants. Observations of ants visiting inflorescences of *Aspasia principissa* and occupying *C. bilamellatum* showed that the ant assemblages were species-rich, indicating that these are general rather than species-specific mutualisms. The generalized pattern of ant occupation of *C. bilamellatum* was not different from that observed for host trees in which orchids did not occur. The results suggest that ant associations are common in lowland Neotropical representatives of the Orchidaceae.

ASSOCIATIONS BETWEEN ants and plants have been described for many groups of plants, and it has been shown frequently that plants will benefit from the presence of ants (Bentley, 1977; Beattie, 1985). These associations appear to be abundant in epiphytes (Beattie, 1985; Davidson and Epstein, in press), where plants were often shown to benefit nutritionally from the presence of ant colonies in roots or in specialized structures that house the ants (Huxley, 1980). In the Orchidaceae, there are many reports of ant associations (Jeffrey, Arditti, and Koopowitz, 1970; Bentley, 1977; Davidson and Epstein, in press), often involving the occupation of some part of the plant by ants. In their study, Jeffrey, Arditti, and Koopowitz (1970) emphasized the importance that these ant associations may have for protection of orchids against insect herbivores.

Because of the large number (over 19,000) of representatives in the Orchidaceae (Atwood, 1986), it is difficult to determine if reports of ant/orchid associations represent a few noteworthy cases or a common theme in the family. Because no study has considered possible ant associations of a number of orchid species in one locality, it is difficult to determine how general these relationships might be. We have investigated 23 species of orchids occurring in the Barro Colorado National Monument in central Panama to determine how many are involved in ant associations. This was largely done by surveying these species for the production of extrafloral nectar and investigating plants for evidences of ant occupation.

Additional information is provided on the nature of ant/orchid associations. For two orchid species, we describe the ant species involved in the associations and the frequency with which orchids are attended or occupied by ants. For one of these orchids, we indicate the degree to which the distribution of ant occupation among plants is similar to that in the general environment.

METHODS—Barro Colorado National Monument (BCNM) is a protected area of lowland, semideciduous tropical forest, located in the Panama Canal in central Panama, consisting of a central island, Barro Colorado Island (BCI), and three adjacent mainland peninsulas. See Croat (1978) and Leigh, Rand, and Windsor (1982) for detailed descriptions of BCI. Croat (1978) lists 90 orchid species that occur on BCI, but well over half of these are listed as rare. Our data for 23 orchid species thus represents a substantial portion of the orchid flora in the area. Orchid nomenclature follows Croat (1978), except *Brassavola nodosa* (L.) Lindley, which occurs on one of the mainland peninsulas of the BCNM but not on BCI.

Production of extrafloral nectar by orchids from the BCNM was studied in several ways. Most in-

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formation was collected from plants in live collections on BCI, with additional observations of orchids at nearby Summit Gardens and in the field. Usually, extrafloral nectar production was observed directly by excluding ants, but the presence of ants was sometimes used as an indication of extrafloral nectar production when the ants were observed feeding from the plants.

Ants attending or occupying two orchid species, *Aspasia principissa* and *Caularthron bilamellatum*, were studied in detail. Ants attending extrafloral nectaries of 14 plants of *Aspasia principissa* were censused once every five weeks during the day using plants occurring near ground level along or near trails on BCI. On the last census date, ants were collected from 13 remaining, active inflorescences. More extensive data were collected for the ants occupying pseudobulbs of *Caularthron bilamellatum*. Ants were sampled over a five-month period from 573 orchids occurring on 87 trees and from 44 trees unoccupied by orchids. All sampled trees were *Annona glabra* L. occurring along the shoreline of the BCNM. Frequencies of ant occurrence among orchids and trees were compared using the log-likelihood ratio, G, an analog to the chi-square test (Sokal and Rohlf, 1981).

RESULTS AND DISCUSSION—Of the 23 species of orchids investigated, 16 species were observed to produce extrafloral nectar (Table 1). All 16 species were found to produce nectar on reproductive structures; nectaries were always found on developing inflorescences (Fig. 1-3) and often found on mature flowers (Fig. 4) and fruits. Nectar was most often produced at the base of pedicels (Fig. 3, 4) or at the bases of the dorsal sepal (Fig. 4) or lateral sepals (Fig. 1).

Of the 16 species producing extrafloral nectar on reproductive structures, 10 also produced nectar on developing shoots (Table 1, Fig. 5). However, only one species, *Caularthron bilamellatum*, produced extrafloral nectar on mature shoots. Interestingly, this is the only species in the study in which the ants occupy any portion of the plant (Dressler, 1981). Although we were unable to collect information for *Epidendrum imatophyllum* or *Coryanthes speciosa*, these might also be expected to produce extrafloral nectar on mature shoots, since ants commonly build nests among the roots of these two species (Jeffrey, Arditti, and Koopowitz, 1970; Croat, 1978).

In most cases, no specialized structures were observed to be associated with the production of nectar. Exceptions were noted for *Caularthron bilamellatum*, which commonly has two or three small, nectar-producing "pits" at the base of the leaves, and in *Aspasia principissa*, which has quite obvious nectaries at the bases of the lateral sepals (seen in the developing bud, Fig. 1).

TABLE 1. *Orchid species from Barro Colorado National Monument, Panama, investigated for the production of extrafloral nectar. The symbol + denotes presence of extrafloral nectar and − denotes absence of extrafloral nectar.*

Species	Reproductive Structures	Developing Shoots	Mature Shoots
Aspasia principissa	+	−	−
Brassavola nodosa	+	+	−
Brassia caudata	−	−	−
Catasetum viridiflavum	+	+	−
Caularthron bilamellatum	+	+	+
Cochleanthes lipscombiae	−	−	−
Dimerandra emarginata	+	+	−
Encyclia chacaoensis	+	+	−
Epidendrum nocturnum	+	+	−
Epidendrum radicans	+	+	−
Gongora quinquenervis	+	+	−
Gongora tricolor	+	+	−
Ionopsis utricularioides	−	−	−
Lockhartia acuta	−	−	−
Masdevallia livingstoneana	−	−	−
Notylia pentachne	+	−	−
Oncidium stipitatum	+	+	−
Pleurothallis brighamii	−	−	−
Pleurothallis grobyi	−	−	−
Pleurothallis spp.	−	−	−
Scaphyglottis graminifolia	+	−	−
Trigonidium egertonianum	+	+	−
Vanilla planifolia	+	−	−

From the viewpoint of plants, two hypotheses are generally considered to explain the occurrence of ant/plant mutualisms (Beattie, 1985): increased nutrition of plants by the presence of ant colonies, and protection of plants by ants against herbivores. These hypotheses are not mutually exclusive. With the exception of *Caularthron* in this study, in which ants colonize the hollow pseudobulbs, nutritional benefit can be excluded to explain the ant/orchid associations implied by the production of extrafloral nectar. Detailed observations of *Aspasia principissa* offered no evidence of ant occupation, while in *Catasetum viridiflavum*, only three of 50 plants harvested from the forest canopy and shoreline were observed to have ant colonies in the root masses (J. K. Zimmerman, pers. obs.). None of the other orchids has specialized structures to house ants or (more circumspectly) was observed to have ants living among the roots.

Ants were frequently observed to attend extrafloral nectaries on inflorescences or developing shoots in the orchids we studied. In *Aspasia principissa*, regular observations indicated that 70% of inflorescences were visited by ants at any given time (Fig. 6). For *Caularthron bilamellatum*, 85% of plants were occupied by ants.

Some studies have considered the effects of ants on the reproductive success of orchids. Rico-Gray and Thien (1986) have shown that the degree to which ants affect the reproductive success of

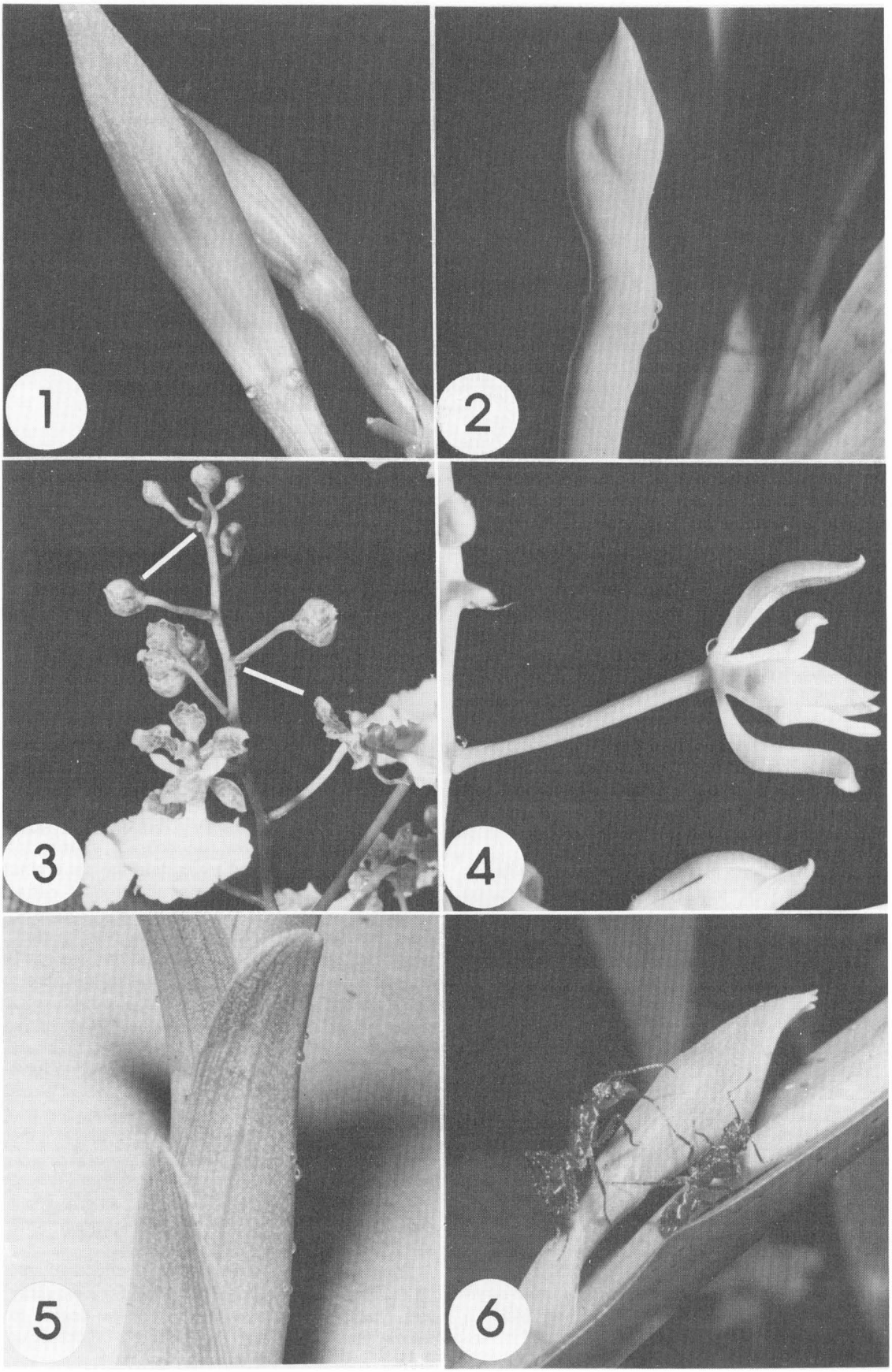
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TABLE 2. *Ant species associated with two orchid species in Barro Colorado National Monument, Panama.*

Orchids: Family	*Aspasia principissa* Species	*Caularthron bilamellatum* Species
Dolichoderinae	*Azteca* sp. 1	*Azteca chartifex* Forel
	Azteca sp. 2	*Azteca instabilis* Forel
	Hypoclinea bispinosa Olivier	*Azteca velox* Forel
		Azteca sp.
		Hypoclinea bispinosa Olivier
		Hypoclinea lutosa F. Smith
Formicinae	*Camponotus* sp. 1	*Camponotus abdominalis* Fabricius
	Camponotus sp. 2	*Paratrachina pubens* Forel
	Paratrechina sp.	
Ponerinae	*Ectatomma ruidum* Roger	*Odontomachus brunneus* Patton
	Ectatomma tuberculatum Olivier	*Odontomachus laticeps* Roger
	Pachycondyla sp.	
Myrmicinae	*Crematogaster* sp. 1	*Crematogaster brevispinosa* Mayr
	Crematogaster sp. 2	
	Pheidole sp.	
	Tapinoma sp.	

Schomburgkia tibicinis (ants occupy the pseudobulbs in this species) is dependent on the ant species associated with individual plants. Fisher (in prep.) found that the presence of ants in pseudobulbs did not affect fruit set in *Caularthron bilamellatum*. More experimental studies are necessary to show that orchids receive protective benefits from the presence of ants, particularly in those where ants do not nest in association with the plants.

Our observations of ant/orchid interactions in *Aspasia principissa* and *Caularthron bilamellatum* suggest these are general rather than species-specific associations. This is indicated by data on ant species found in association with these two orchid species (Table 2; see also Rico-Gray and Thien, 1986). All 13 inflorescences of *Aspasia principissa* were found to have different species of ants attending them (Table 2). In general, the same species of ant was observed at the same inflorescence over a five-week observation period, indicating that ants were recruiting to the orchids from nearby colonies.

In *Caularthron bilamellatum*, plants were occupied by 11 species of ants (Table 2). For individual plants, the ants occupying orchids could only be identified to the genus level. However, the following trends could be identified when data for orchids found on *Annona glabra* were compared to the same species of host trees unoccupied by orchids (Table 3). Most of the ants occupying orchids were of the genus *Azteca* (84%), a proportion not different from that of ant-occupied trees without orchids (89%; $G = 0.966$, $p = 0.41$, $df = 1$). Data for other genera of ants were too few to make any comparisons. The proportion of unoccupied orchids (15%) was also not different from that observed for host trees (14%; $G = 0.096$, $p = 0.72$, $df = 1$). Overall, these data indicate that the ants associated with *Caularthron bilamellatum* were similar to those in the general shoreline environment (Table 3).

TABLE 3. *Frequency of ant occupation of the orchid* Caularthron bilamellatum *and that of host trees (*Annona glabra*) on which the orchids did not occur. Distribution of ant occupation among orchids was not different from that among host trees.*[1]

	Azteca	Other Ant Species	Unoccupied	Total
Orchids	406	79	88	573
Trees	34	4	6	44
Total	440	83	94	617

[1] $G = 1.063$, $p = 0.61$, $df = 2$.

The lack of specificity in these ant/orchid associations is similar to that described for forest herbs in the genus *Costus* described by Schemske (1982) from BCI. Many of the genera and species of ants found in association with *Aspasia* and *Caularthron* were also found to visit *Costus* inflorescences (Schemske, 1982).

In conclusion, we found that the production of extrafloral nectar was common among several orchid species from a lowland, Neotropical forest site, while ant occupation of plants was relatively uncommon. It appears likely, with exceptions, that extrafloral nectar production functions to attract ants, which protect the orchids from insect herbivores. However, we emphasize the need for experimental studies of the potential benefits orchids may derive from ant attendance. Available evidence indicated that ant/orchid associations are probably very general, rather than specific, mutualisms. Comparative data from other localities would be useful to determine the commonness of ant/orchid

Fig. 1-6. Extrafloral nectaries in orchids. **1.** Extrafloral nectaries on developing flower buds of *Aspasia principissa*. **2.** Production of extrafloral nectar by developing inflorescence of *Catasetum viridiflavum*. **3.** Extrafloral nectar production on an inflorescence of *Oncidium stipitatum*. **4.** Extrafloral nectar on a mature flower of *Notylia pentachne*. **5.** Extrafloral nectar on developing shoot of *Catasetum viridiflavum*. **6.** *Ectatoma tuberculatum* defending developing flower buds of *Aspasia principissa*.

associations better, particularly from areas of higher elevations, where ants may be less abundant (Koptur, 1985).

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