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**FLOWER ECOLOGY IN THE NEOTROPICS:
a flower-ant love-hate relationship**

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ABSTRACT

A quantitative comparative study of ants visiting flowers in the canopies of savanna and forest in the upper Orinoco (Venezuela) showed that flowers in the savanna are more likely to display features for avoiding ant visits than do flowers in the forest canopy. In both, savanna and forest canopy, some flowers have special features to attract ants, probably to reduce herbivore pressure, whereas others possess features that hinder the access of ants to the flowers. The number of plant specimens, and of species, having flowers of the former type, is more abundant in forest canopy; whereas the latter type is predominant in the savanna.

INTRODUCTION

It has been commonly assumed that flowers somehow repel ants or make access to their reproductive parts difficult for them (Janzen, 1977; Guerrant & Fiedler, 1981; Herrera *et al.* 1984; Koptur & Truong 1998). However, the opposite often occurs, as several flowers have specialized features to attract ants. For example, the orchid *Spathoglottis plicata* Blume attracts ants using nectaries strategically placed on the base of flowers and on flower buds (Jaffe *et al.*, 1989), presumably to reduce herbivory on its flowers. Although there is an extensive literature on ant-plant relationships (see extensive reviews in Jolivet, 1996, for example), not much is known about ant-flower relationships.

Plants produce flowers, in principle, for sexual reproduction. The adaptive value of flowers is to attract a specific species or a range of specific pollinators. In doing so, they offer nectar, pollen, and scent, and display odors, shapes and colors as reinforcing stimuli to attract pollinators.

Although ants are known to pollinate plants, especially orchids (Peakall, 1994), ants are poor pollinators, partly due to the fact that they do not fly and thus are very ineffective dispersers of pollen. Moreover, ants produce various antibiotics in their different exocrine glands that inhibit pollen germination (Beattie *et al.*, 1984). Ants are known as generalist foragers, exploiting any resource available, especially nectars and sugary secretions from plants and animals. Thus, ants are potential exploiters of flower nectar, and plants have evolved mechanism to prevent ants from distracting resources aimed at pollinators. Chemical flower repellents exist (Van der Pijl, 1954) but seem to be rare (Feisinger & Swarm, 1978), suggesting that plants use other mechanisms to exclude ants from their flowers. The strength of these interactions may vary in different ecosystems. Specifically, ants living in the forest canopy may have evolved stronger adaptations to exploit plants and their flowers than ants living on the ground, which might have wider range of resources at their disposal.

In order to get a closer understanding of the factors that determine the relationship between ants and flowers, in this paper we address the following questions: What are the main strategies flowers have to attract or repel ants? And, Do these strategies differ between plants flowering within the savanna and the forest canopy?

METHODS

We studied the flowers occurring in the upper layer of the savanna (“savanna canopy”) consisting of grasses, bushes and herbs, growing on sandy soils on a 5 ha plot next to the Humboldt Station at La Esmeralda, Estado Amazonas, Venezuela (3°9' N, 65°36' W). The savanna is of the type described for the Guyana Highlands by Huber (1986), with a characteristic low occurrence of Graminaceae species. Most of the savanna is flooded once a year and burns in average every two years. Precipitation and temperature fluctuations in La Esmeralda are undistinguishable from that at Surumony. The forest canopy study was performed at the Surumoni project, located in the upper Orinoco region, Estado Amazonas, Venezuela, close to the black water river Surumoni, at an elevation of about 110 m (3°10' N, 65°36' W). The plot contains floodable and non-floodable tropical lowland forest (*terra firme*) on sandy soils. Mean annual rainfall is about 2700 mm, with a pronounced seasonality, and the average temperature is 26.5°C (further details in Szarzynski & Anhuf, 2001; Nieder *et al.*, 2001). A modified commercial crane with a swingable boom of 40 m, mobile on a 120 m rail, was set up in 1996. Researchers are able to reach the outer canopy layer in an area of 1.4 ha with an observation gondola (Blüthgen *et al.*, 2000).

Plants were visited at day and night. The time when flowers opened was classified as Am (6-9 Am) and Pm

(3-5 Pm) and this time interval was used to count the ants on the flowers of the plant. Times between 10 AM and 2 PM were extremely hot at the savanna with ant activity close to zero. Pollinator activity was assessed at these same time intervals. The flowers were classified into 3 categories, according to the number of ants found on or near them (see results). Control sticks chosen in the savanna consisted of dry flower stems standing at the average height of the savanna canopy. In the forest, control sticks consisted in dry terminal branches of trees. The dates of visits made to both sites simultaneously were: 23-31/03/1997, 28/7-18/8/1997, 17-28/8/1999, 15-21/7/1999, 2-7/3/2000, comprising a minimum of 90 hours of observation for each habitat (savanna and forest canopy), which were performed by the same pair of observers in each visit, but which differed between visits.

RESULTS

The plants surveyed in the savanna were mostly grasses, herbs and small shrubs. Besides the flowering plants reported in Table 1, the savanna contained small *Byrsonima* sp. trees (Malphiaceae), which appear to have permanent associations with ants and were not further studied here. The plants found in the forest at Surumoni were trees and lianas. The species composition of both sites for both plants and ants was completely different (Tables 1 and 2).

In each, savanna and forest, we grouped the flowers (or inflorescences) into three distinct functional categories.

Category 1: Flowers that repel ants. Visits by ants to these flowers are lower than visits to a control wooden stick placed nearby. Alternatively, we might group flowers into this category if the number of ant visits to flowers were located in the lower quartile of that for all flowers sampled in that habitat. Both methods classified the same samples into category 1. These flowers have either physical or chemical structures that deter ants from visiting them. A clear example is *Chamaecrista desvauxii*, which is pollinated by large bumble bees and thus produces large amounts of nectar. This plant protects its flowers from ants and other insects by secreting a sticky substance all along its stems, branches and leaves. Another example are *Polygala* spp. which display their flowers on long, very thin, and waxy pseudo-stems, making it difficult for walking insects to access the flowers.

Category 2: Flowers with no distinct feature for either attracting or repelling ants. Ants visit these flowers with the same frequency as they visit a control empty wooden stick placed nearby).

Category 3: Flowers that attract more than twice the number of ants than that attracted to control sticks. Another way of grouping flowers into this category is if over twice the number of ants were attracted to the flower of inflorescence, compared to the mean number attracted by all flower species sampled in that habitat. The attraction signal consisted mostly in “extrafloral” nectaries on the flower stems, at the base of the inflorescence or flower or at the external part of the calyx. For example, flowers of *Irlbachia* spp. have nectaries on the base of the flowers and on the flower stems, and secrete nectar when the flower is in bud or recently open. Some flowers found on the forest canopy that were classified into this category could have been classified as flowers of category 2, because we found no special feature for the attraction of ants on the flowers, however, we classified them as category 3, because large numbers of ants were found on the flowers, possibly because they were nesting nearby or were tending hemiptera feeding on the flower stems.

The frequency of ants visiting the control was much higher in the forest than in the savanna. The flower, as classified with the three categories, in the savanna is indicated in Table 1, whereas that of the flowers in the canopy is given in Table 2. The frequency of occurrence of the different categories of flowers differs widely in savanna compared to the canopy. In Figure 1a, we observe that most species in category 1 occurred in the savanna, whereas species in category 2 and 3 were more common in the forest canopy. A similar pattern could be observed when analyzing the total abundance of the flowers per category (Figure 1b).

The ant fauna in both sites was different (Tables 1 and 2) and so was the proportion of ants distributed among the three categories. If we compare the number of plant species in category 1 and 3 between both ecosystems with a Chi-square test, we obtain: $X^2 = 8.96$, $p = 0.0028$. The same comparison between the number of flower samples found in each category gives the results: $X^2 = 77.0$, $p < 0.00001$. The most common ant species encountered in the forest was *Cephalotes atratus* (Linnaeus), whereas in the savanna *Camponotus* spp., *Ectatomma* spp. and *Crematogaster* spp. were the most common.

DISCUSSION

Coevolution, as defined by Ehrlich and Raven (1964) and elaborated by Janzen (1980) is a process by which two organisms develop a close association over evolutionary time, by means of a series of reciprocal steps. Ehrlich and Raven developed this theory using the tight relationship between some butterflies and their host plants, and since then the theory of co-evolution has been proposed as an explanation for the evolution of associations between many pairs of groups of organisms (Gilbert, 1983; Dettner & Liepert, 1994). Evidence to the contrary, i.e. independent evolution of traits that allow for a close relationship between different types of organisms, has also accumulated (Jermy, 1976; Janzen, 1980; Miller, 1987; Fox 1988). Coevolution implies that each member of the association directly influences the evolution of the other organism. Thus, in a plant/herbivore system, not only does the herbivore influence the evolution of the plant, but the plant also influences the evolution of the herbivore. With this perspective, a broad and lax coevolutionary process between plant flowers suffering nectar robbing by ants and that of ants trying to exploit resources provided by flowers can be imagined. These two simultaneously occurring evolutionary processes may not necessarily qualify as coevolution, but may be considered as an arms race between flowers and ants, where flowers sometimes switch to cooperation with ants, when repelling them is impossible.

Our results suggest that flowers in the savanna are less indifferent to ants than those in the forest canopy. More plant species and more plants in the savanna repel ants than do flowers in the forest canopy studied. The most common mechanism flowers in the savanna use to make themselves inaccessible to ants, is the production of long, thin and waxy flower pseudo-stems, making access to the flowers difficult for ants that normally walk on sand (Federle *et al.* 2000). This hiding mechanism does not seem to be available to flowers in the forest canopy, as arboreal ants are harder to stop from climbing thin stems. Most ants in the canopy collect homopteran honeydew (Blüthgen *et al.* 2000) and thus are more likely to enter flowers in search of homopteran insects or plant nectar.

Other mechanisms flowers have to avoid ants taking their nectar involve hiding the nectar in special organs, available only to birds or bats, or dispensing from nectar altogether, attracting the pollinator by offering only pollen or scent. The prevalence of ant avoidance mechanisms in the savanna compared to the forest canopy suggests that access to water limits nectar production in the savanna. On the other hand, arboreal ants seem to be more difficult to keep at bay than soil-dwelling ants. Thus, flowers in the canopy are probably more tolerant to ants, dispensing from repulsive mechanisms against them. One morphological feature that might provide a basis for this difference is that flowers in the forest canopy are more abundant, more globular in form and more accessible, than those in the savanna, which are rather few and more tubular in shape. In Spain, Herrera *et al.* (1984) found that globular accessible flowers were three times more likely to be visited by ants than tubular ones. They also showed that inflorescence with abundant flowers showed more ant visits than those with one or few flowers. On the other hand, globular flowers having a bowl shape suffer relatively more desiccation than those that have a tubular shape (Kevan & Baker, 1983) and thus, in globular flowers, the nectar crystallizes much faster. These different environmental constraints may be correlated to the significantly higher levels of histidine found in nectars of herbaceous plants compared to threes and lianas by Baker and Baker (1973).

Ants might benefit plants and their flowers by providing protection against herbivores. Some plants might even use ants as pollinators (Proctor *et al.*, 1996), although this is not very likely for trees. Thus, plants may attract (“domesticate”) certain ant species providing this protection to the flowers. It would seem that plants in the forest are more likely to have “domesticated” ants than their counterparts in the savanna, although further detailed ecological, morphological and physiological studies on the ant-flower interactions are needed in order to better understand these ecological interactions.

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Table 1: Pattern of ant visit in savanna flowers of La Esmeralda. The species are ordered according to the number of ants visiting the flowers or inflorescence:

Family	Plant species	No. of ants /flower/min	Ant species	Possible pollinator	Time flower opens	Nr of flowers	Category
naceae	<i>Irbachia alata</i>	3.40	<i>Camponotus</i> sp. <i>Pheidole</i> sp. <i>Crematogaster</i> sp. <i>Ectatomma ruidum</i> <i>Cephalotes pussilus</i>	?	Am/Pm	10	3
naceae	<i>Irbachia</i> sp. 1	2.29	<i>Camponotus</i> sp. <i>Paratrechina</i> sp.	Bats	Am	14	3

			<i>Pseudomyrmex simplex</i>				
omataceae	<i>Tibanchina aspera</i>	1.93	<i>Camponotus sp.</i>	Halictinae	Am	15	3
laceae	<i>Pitcairnia armata</i>	0.42	<i>Ectatomma ruidum</i>	Collibri (Aves)	Am	12	2
				Apidae			
lpinaceae	<i>Chamaecrista desvauxii</i>	0.08	<i>Crematogaster sp.</i>	Aplidae	Am	7	1
laceae	<i>Polygala sp. 1</i>	0.05	<i>Pheidole sp.</i>	?	Am/Pm	6	1
omatacea	<i>Macaيرا sp. 1</i>	0.02	<i>Ectatomma tuberculatum</i>	?	Am	>20	1
laceae	<i>Polygala sp. 2</i>	0	-	Coleoptera	Am/Pm	>20	1
laceae	<i>Polygala sp. 3</i>	0	-	?	Am	>20	1
omataceae	<i>Miconia sp. 1</i>	0	-	Chrisomelidae	Pm	3	1
omataceae	<i>Pterogasta divaricata</i>	0	-	Curculionidae	Am/Pm	29	1
aceae	<i>Bulbostylis junciformis</i>	0	-	?	Am/Pm	5	1
aceae	<i>Rhynchospora globosa</i>	0	-	?	Am/Pm	5	1
aceae	<i>Rhynchospora barbata</i>	0	-	?	Am/Pm	5	1
ceae	<i>Xyris sp. 1</i>	0	-	?	Pm	>20	1
ROL	Wooden stick	0.1	<i>Camponotus sp.</i>	-	Am/Pm	20	2

Table 2: Pattern of ant visit in canopy flowers at Surumoni. The species are ordered according to the number of ants visiting the flowers.

Family	Plant species	No. of ants / flower/ min	Ant species	Time	Nr of flowers open	Category
Caesalpinaceae	<i>Tachigali guianensis</i>	30	<i>Aztecasp.</i>		1	3
Vochysiaceae	<i>Vochisia obscura</i>	15	<i>Azteca sp.</i>	Am/Pm	9	3
			<i>Camponotus sp.</i>			
			<i>Pseudomyrmex simplex</i>			
			<i>Cephalotes atratus</i>			
Caesalpinaceae	<i>Chamaecrista negrensis</i>	6	<i>Azteca sp.</i>		1	3
Caesalpinaceae	<i>Sclerobium sp.</i>	>5	<i>Camponotus sp.</i>	Am/Pm	8	3
			<i>Cephalotes atratus</i>			
			<i>Procryptocerus sp.</i>			
			<i>Pseudomyrmex simplex</i>			
			<i>Pseudomyrmex sp.</i>			
			<i>Dolichoderus bidens</i>			
Vochysiaceae	<i>Qualea trichanthera</i>	>5	<i>Pseudomyrmex flavidus</i>	Am/Pm	6	3
			<i>Pheidole sp.</i>			
			<i>Crematogaster sp.</i>			
			<i>Camponotus sp.</i>			
			<i>Solenopsis sp.</i>			
			<i>Daceton armigerum</i>			
			<i>Cephalotes atratus</i>			

Figure 1:
 Percentage of plant species observed (a) and percentage of individual plant specimens observed (b), assigned to categories 1, 2 or 3 with regard to

ant visit to flower. Category 1: repels ants, 2: indifferent to ants, 3: attracts ants. Open bars: savanna flowers, closed bars: canopy flowers.



