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Interaction Between Ants and Plants Bearing Extrafloral Nectaries in Cerrado Vegetation

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Interações entre Formigas e Plantas com Nectários Extraflorais na Vegetação do Cerrado

RESUMO - Nectários extraflorais (NEFs) são glândulas de néctar não relacionadas com o processo de polinização da planta e que podem ocorrer virtualmente em todas as estruturas vegetativas e reprodutivas de angiospermas. Estudos recentes revelaram que NEFs ocorrem em diversas espécies de arbustos e árvores dos cerrados brasileiros. Plantas portadores destas glândulas são visitadas de dia e de noite por diversas espécies de formigas nectarívoras do cerrado. Nesta revisão apresentamos os dados obtidos nos últimos 15 anos sobre a interação entre formigas e plantas com NEFs em vegetação de cerrado. Estudos experimentais no campo indicam que as formigas visitantes de NEFs podem predar ou injuriar insetos herbívoros que encontram sobre as plantas, reduzindo significativamente as taxas de herbivoria sobre as folhas, botões ou flores. Em resposta, algumas espécies de herbívoros desenvolveram vários mecanismos para evitar o ataque das formigas sobre suas plantas hospedeiras. Os benefícios oferecidos às plantas pelas formigas visitantes, entretanto, podem variar com a agressividade da espécie de formiga, com as estratégias defensivas apresentadas pelos insetos herbívoros, bem como com a espécie de planta. Os resultados obtidos para diferentes espécies de plantas de cerrado são discutidos, indicando áreas promissoras para estudos experimentais futuros.

PALAVRAS-CHAVE: Insecta, Hymenoptera, herbivoria, mutualismo, predação.

ABSTRACT - Extrafloral nectaries (EFNs) are nectar-secreting glands not directly involved with pollination which may occur on virtually all above-ground plant parts of angiosperms. Recent studies revealed that such glands are widely distributed amongst the woody flora of the Brazilian cerrados. Plants bearing EFNs are visited day and night by a diverse assemblage of nectarivorous ants. In this review we present the data gathered during the past 15 years on the interaction between ants and EFN-bearing plants in cerrado vegetation. Field experiments indicate that ants visiting EFNs may prey or attack insect herbivores on the plant foliage, significantly reducing herbivore damage to leaves, buds or flowers. As a response, some herbivore species have developed an array of mechanisms to circumvent the ants' deterring capacities on their host

plants. Ant-derived benefits to plants, however, may vary with the species of visiting ant, with the defensive tactics of the associated herbivores, as well as with the plant species. We discuss the results obtained for different cerrado plant species, and suggest some promising topics for future experimental investigation.

KEY WORDS: Insecta, Hymenoptera, herbivory, mutualism, predation.

"The hypothesis of intimate mutualistic relations between ants and the higher plants is one of those fascinating constructions in which certain gifted and imaginative botanists have rivalled the inventors of the mimicry hypothesis in the zoological field. Both of these constructions have been treated as facts of the utmost value in supporting a still more general hypothesis - that of natural selection, and both, after having been carried to extremes by their respective adherents, are now facing the reaction that is overtaking Neodarwinism. Authors like Fritz Müller, Schimper, Huth, Delpino, Beccari and Heim have marshalled a formidable array of observations in favor of the view that many plants develop elaborate structures to be used as lodgings by certain pugnacious ants or even furnish these insects with exquisite food substances, and in return for these services are protected by their tenants from the leaf-cutting ants or from other leaf-destroying animals. These observations are now being subjected to critical revision by authors like Rettig and H. von Ihering, whose attitude toward the whole suject is avowedly skeptical and reactionary. It behooves us therefore to examine both sides of the argument and, if possible, to adopt a position which will favor and not forestall further investigation."

(William M. Wheeler, 1910)

The natural history of ant-plant associations has attracted the attention of biologists around the world for nearly two centuries. During this time it became evident that ants and plants can affect each other's lives in diverse and complex ways. Although the sug-gestion of mutualistic interactions between ants and plants is present in the classic works of naturalists such as Belt (1874), Delpino (1875), and Trelease (1881), at that time the supporting evidence was based mostly on detailed anatomical and/or behavioral observations rather than experimental demonstration. In fact, as shown in the opening paragraph quoted from Wheeler's book on ants (see above), this theme stimulated a considerable amount of debate among early naturalists. Despite the wide taxonomic and geographical distributions of myrmecophilous plants (Bequart 1922, Wheeler & Bequart 1929, Wheeler 1942), and their intrinsic biological importance, it was not until about three decades ago that the pioneering field studies of Janzen (1966, 1967, 1969) provoked a burst of research on ant-plant interactions by ecologists around the world. Since then many excellent experimental field studies have been conducted, embracing a wide variety of ant-plant systems from many kinds of environments (reviewed by Davidson & McKey 1993).

With the exception perhaps of the so-called harvester ants which store and consume seeds (Beattie 1995), and the leaf-cutting ants which may severely defoliate both native and cultivated plants (Vander Meer et al. 1990), many ant taxa are known to maintain facultative or obligate mutualisms with many species of angiosperms from different families (see Bentley 1977, Buckley 1982, Koptur 1992, Hölldobler & Wilson 1990, Schupp & Feener 1991, Davidson & McKey 1993). Experimental field studies have shown that plants may benefit from interacting with ants

in basically five ways (after Beattie 1985): (1) the ants protect the plant against herbivores; (2) the ants promote the growth and survival of the host plant by pruning foliage of neighboring plants; (3) the ants feed the plant with essential nutrients; (4) the ants disperse seeds and fruits; (5) the ants pollinate the plant. In exchange for these services, ant-associated plants usually produce two main rewards for the ants — nest site and/or food.

Research on ant-plant interactions has developed enormously in the past decades, and the recent literature is rich in studies dealing with a diversity of aspects underlying such associations both in temperate and tropical habitats. The current state of the knowledge in this field can be assessed in the excellent reviews by Beattie (1985), Jolivet (1986), Hölldobler & Wilson (1990), Koptur (1992) and Davidson & McKey (1993).

In the present paper we are mostly concerned with the facultative associations involving ants and plants bearing extrafloral nectaries, and their effects on the associated insect herbivores. We will provide a review of the data gathered during the past fifteen years in the cerrado vegetation of Brazil, and suggest some promising topics for future research in the area.

The Taxonomic Distribution and Abundance of Extrafloral Nectaries in Cerrado Vegetation

Extrafloral nectaries are nectar-secreting organs not directly involved in pollination, although they may occur near the reproductive parts of the plant (Bentley 1977). Such glands are extremely variable morphologically and anatomically, being found on virtually all above-ground plant parts such as the leaf blade, petiole, rachis, stipules, stem, bracts, sepals, petals, fruits, and cotyledons (Bentley 1977, Elias 1983, Oliveira & Leitão-Filho 1987, Koptur 1992, Morellato & Oliveira, 1994). Chemical analyses of the extrafloral nectar secreted by different plant taxa have revealed that the aqueous solution may contain sugars, amino acids, proteins, lipids, and vestigial amounts of other organic compounds (Bentley 1977, Baker & Baker 1975, 1983).

Extrafloral nectaries are widely distributed among the angiosperms of both tropical and temperate regions, although they are more commonly found in the flora of tropical areas. Quantitative floristic surveys from nine different cerrado areas in the States of São Paulo (Oliveira & Leitão-Filho 1987) and Mato Grosso (Oliveira & Oliveira-Filho 1991) showed that EFNs are particularly common amongst the woody flora (shrubs and trees) of this vegetation type (Table 1). A total of 44 EFN-bearing species from 17 families were sampled in the cerrados of São Paulo and Mato Grosso. The plant families most frequently having EFNs are the Mimosaceae (7 species), Bignoniaceae (6 species) and Vochysiaceae (5 species). Nectaries associated with vegetative parts such as leaves and stem were much more common (41 of 44) than those located near the bud or flower (7 of 44; see Table 1).

Data on proportion and abundance of plant species bearing EFNs in the woody flora of the nine surveyed cerrado areas of São Paulo and Mato Grosso are summarized in Table 2. EFNs were present in 15-22% of the species sampled in the cerrado areas of São Paulo, with local abundances ranging from 8 to 20% of the woody individuals (Oliveira & Leitão-Filho 1987). In Mato Grosso, nectariferous species comprised 21-26% of the sampled flora and accounted for 22-31% of the shrubs and trees recorded (Oliveira & Oliveira-Filho 1991). In general the values obtained in cerrado areas (Table 2) are higher that those from temperate habitats, and tend to support the contention that EFNs are more common in tropical than in temperate floras (see also Bentley 1977, Keeler 1979a, b, 1980, 1981a, b, Pemberton 1988, Schupp & Feener 1991, Coley & Aide 1991, Morellato & Oliveira 1991, Koptur 1992).

Ants, Extrafloral Nectaries, and the Protectionist Hypothesis

Ants outnumber all other terrestrial ani-

Table 1. Plant species bearing extrafloral nectaries in cerrado vegetation. Data are based on surveys of woody plants conducted by Oliveira & Leitão-Filho (1987) in five cerrado areas in the state of São Paulo, and by Oliveira & Oliveira-Filho (1991) in four areas in the state of Mato Grosso. Only shrubs and trees with a basal trunk diameter of at least 3 cm were included in the surveys.

Plant species	Site of nectary	Plant species	Site of nectary
BIGNONIACEAE		MARCGRAVIACEAE	
Arrabidaea brachipoda	leaf blade	*Norantea guianensis*	leaf blade
Cybistax antisyphillitica	leaf blade	MIMOSACEAE	
Jacaranda cuspidifolia	leaf blade	*Anadenantera falcata*	rachis
Tabebuia aurea	leaf blade	*Enterolobium gummiferum*	rachis
Tabebuia caraiba	leaf blade	*Inga uruguensis*	rachis
Tabebuia ochracea	leaf blade	*Inga heterophylla*	rachis
BOMBACACEAE		*Mimosa xanthocentra*	rachis
Eriotheca gracilipes	petiole	*Plathymenia reticulata*	rachis
CAESALPINACEAE		*Stryphnodendron adstringens*	rachis
Bauhinia rufa	intrastipular trichomes	*Stryphnodendron obovatum*	rachis
Cassia rugosa	rachis	*Stryphnodendron polyphyllum*	rachis
Cassia speciosa	rachis	MYRSINACEAE	
CARYOCARACEAE		*Rapanea guianensis*	leaf blade
Caryocar brasiliense	calyx	*Rapanea lancifolia*	leaf blade
CHRYSOBALANACEAE		OCHNACEAE	
Hirtella gracilipes	leaf blade	*Ouratea castanaefolia*	stipules
Hirtella hoehney	leaf blade	*Ouratea hexasperma*	stipules
Licania humilis	leaf blade	*Ouratea spectabilis*	stipules
COMBRETACEAE		ROSACEAE	
Terminalia argentea	petiole	*Prunus sellowii*	leaf blade
Terminalia brasiliensis	petiole	RUBIACEAE	
Terminalia fagifolia	petiole	*Tocoyena brasiliensis*	calyx
Terminalia subsericea	petiole	*Tocoyena formosa*	calyx
EBENACEAE		VERBENACEAE	
Diospyrus coccolobifolia	leaf blade	*Aegiphila lhotzkiana*	leaf blade
EUPHORBIACEAE		*Aegiphila sellowiana*	LEAF BLADE
Hieronyma alchorneoides	leaf blade	VOCHYSIACEAE	
Richeria grandis	petiole	*Callisthene fasciculata*	stem
LYTHRACEAE		*Qualea dichotoma*	stem, pedicel
Lafoensia paccari	leaf blade	*Qualea grandiflora*	stem, pedicel
MALPIGHIACEAE		*Qualea multiflora*	stem, pedicel
Heteropteris acutifolia	leaf blade	*Qualea parviflora*	stem, pedicel
Heteropteris byrsonimifolia	leaf blade		

mals (Wheeler 1910) and the colonies of some species may contain over 20 million individuals (Wilson 1971). The dominance of ants is particularly conspicuous in tropical habitats such as the Amazonian rain forests, where these insects may account for nearly 70% of the individual arthropods found on the forest canopy (Tobin 1991). The diversity of arboreal ants in tropical localities is equally impressive — a single tree in a Peruvian Ama-

Table 2. Occurrence and abundance of woody plants with extrafloral nectaries in cerrado areas of São Paulo and Mato Grosso.

Area	No. of species sampled	Percentage with EPNs sampled	Percent cover of plants with EFNs
São Paulo[a]			
Itirapina	117	15.4	17.5 (879/5029)
São Simão	65	20.0	18.6 (426/2295)
Mogi-Guaçu	104	20.2	20.3 (1920/9435)
Moji-Mirim	103	16.5	15.1 (479/3167)
Luís Antonio	64	21.9	7.6 (262/3428)
Mato Grosso[b]			
Cerrado site 1	64	23.4	28.1 (157/559)
Cerrado site 2	47	25.5	31.2 (74/237)
Cerrado site 3	68	20.6	27.6 (421/1524)
Cerrado site 4	30	23.3	21.6 (39/181)

[a]After Oliveira & Leitão-Filho (1987), based on floristic surveys from: Giannotti and Leitão Filho (1979) (Itirapina); UNICAMP's Graduate Program in Ecology (São Simão); Gibbs *et al.* (1983) (Mogi-Guaçu); Toledo Filho *et al.* (1984) (Moji-Mirim); Toledo Filho (1984) (Luís Antonio).
[b]After Oliveira & Oliveira-Filho (1991).

zon forest may host 43 ant species, which is comparable to the ant fauna occurring in all of the British Isles (Wilson 1987). Such a remarkable dominance of ants on plant foliage in tropical habitats may suggest that a large part of their diets is comprised by plant-derived food resources, as for example plant nectar (Tobin 1991, Rico-Gray 1993). In fact, as reported above, plants bearing extrafloral nectaries are very common in tropical environments, and although they attract a variety of nectar-feeding insects, ants are by far the most frequent visitors of these glands (Oliveira & Brandão 1991).

Although the controversy on the adaptive significance of extrafloral nectaries (hereafter EFNs) exists for over a century, numerous experimental field studies have provided strong evidence supporting the so-called "protectionist hypothesis" (Brown 1960, Bentley 1977). According to this view, ant visitation to EFNs is beneficial to the plant because the ants' predatory and/or aggressive behavior toward herbivores reduces significantly the damage caused to the plant by the latter. In fact, during the past few years ants visiting EFNs have been demonstrated to increase plant fitness by deterring leaf herbivores (Koptur 1979, Stephenson 1982, Smiley 1985), flower herbivores (Schemske 1980, Horvitz & Schemske 1984, Rico-Gray & Thien 1989), and seed predators (Inouye & Taylor 1979, Picket & Clark 1979). Protection by ants, however, is not universal and there are also studies showing that ants may not benefit EFN-bearing plants (O'Dowd & Catchpole 1983, Heads & Lawton 1984, Whalen & Mackay 1988, Rashbrook *et al.* 1992).

Since extrafloral nectar is a generalized food source which attracts a wide diversity of ant taxa (Oliveira & Brandão 1991), the mutualism between the ants and the plant is usually non-specialized and of a facultative nature (Schemske 1983, Addicott 1984). Therefore the outcome of such EFN-mediated mutualistic associations may vary with factors such as time and habitat type, aggressiveness of ant associates, and the ability of herbivores to overcome ant predation (Koptur

1992, and included references).

Ant Assemblages at Extrafloral Nectaries in Cerrado Vegetation

The ant fauna associated with EFNs has been quantitatively surveyed on three plant species typical of cerrado vegetation: *Qualea grandiflora* (Vochysiaceae), *Caryocar brasiliense* (Caryocaraceae) and *Ouratea hexasperma* (Ochnaceae). Table 3 summarizes the ant genera in each subfamily and the number of species per genus recorded on each of the three plant species. The subfamilies Formicinae and Myrmicinae were the best represented at EFNs. The formicine genus *Camponotus* presented a higher number of species visiting EFNs than the remaining genera recorded on each of the plants censused (Table 3; see also Oliveira & Brandão 1991, Oliveira *et al.* 1995).

The ant censuses conducted on shrubs of *Caryocar brasiliense* and *Ouratea hexasperma* showed that the ants actively collect extrafloral nectar on the plants both day and night (Fig. 1). The species composition of the principal ant visitors, however, changes markedly from one period to the other. The diurnal ant fauna at EFNs of *Caryocar* is dominated by the ants *Zacryptocerus pusillus* (Klug), *Camponotus crassus* and *C.* aff. *blandus*, while the species *Camponotus rufipes* (Fabricius), *C. pallescens* Mayr and *C. renggeri* Emery are the most frequent nocturnal visitors (Fig. 1). A very similar pattern was observed with the principal ant visitors of the EFNs of *Ouratea* (Fig. 1). A detailed account of the ant faunas associated with the EFNs of *Caryocar* and *Ouratea* is given by Oliveira & Brandão (1991) and Oliveira *et al.* (1995), respectively.

Different ant species frequently have distinct humidity and temperature preferences, especially in tropical habitats, which may result in the segregation of the daily foraging schedules by sympatric ant species (Levings 1983, Torres 1984). Ant species replacements at long-lasting liquid food sources (i.e., extrafloral nectar, homopteran honeydew, lepidopteran secretions) have already been reported by several authors, and its possible that such a temporal segregation of foraging activities ultimately reduces interspecific competition among the ants (Hill & Blackmore 1980, Hölldobler 1986, Klotz 1984, Oliveira & Brandão 1991, DeVries 1991, Oliveira *et al.* 1995).

Ants as Anti-Herbivore Agents of Plants with Nectaries: The Evidence in Cerrado Vegetation

Experiments with *Qualea* spp. (Vochysiaceae). The first attempt to test the potential of ants as anti-herbivore agents of nectary plants in cerrado vegetation was performed by Oliveira *et al.* (1987) with *Qualea grandiflora*, a tree species that bears paired EFNs along the stems, next to the insertion of leaves. The results showed that EFNs are important promoters of ant activity on *Q. grandiflora* leaves. Frequency of ant accupancy (i.e., proportion of plants being visited by ants) and mean number of ants per plant were shown to be much higher on *Q. grandiflora* than on neighbouring plants without EFNs. Moreover, using live workers of the termite *Armitermes euamignathus* (Termitidae) as baits for ants on experimental plant pairs, Oliveira *et al.* (1987) demonstrated that: (1) ant visitors to EFNs do attack and remove the termites from leaves of *Q. grandiflora*; (2) increased ant densities on *Q. grandiflora* result in many more termites being attacked by foraging ants on this species than on neighbouring plants lacking EFNs; (3) out of 12 ant species recorded attacking the termites, three common and aggressive *Camponotus* species (*C. rufipes*, *C. crassus* and *C.* aff. *blandus*) clearly showed the greatest potential for herbivore deterrence, together accounting for 87% of the termites attacked on leaves of *Q. grandiflora*. Although these results strongly suggest that visiting ants to EFNs would deter potential herbivores in the cerrado, they were based on experiments with live termites used as simulated herbivores. Therefore additional experiments were

Table 3. Ant genera, by subfamily, observed at extrafloral nectaries from different plant species in cerrado vegetation. Values in parentheses are the number of species. Part of the data from *Caryocar* (7 species in 7 genera) and all data from *Qualea* were obtained using live termite baits. Data from *Caryocar* and *Ouratea* include night-time censuses.

Plant species	Formicinae	Dolichoderinae	Myrmicinae	Ponerinae	Pseudomyrmecinae	Total no. genera (species)	Source
Caryocar brasiliense (Itirapina, SP)	*Camponotus* (10) *Paratrechina* (2) *Brachymyrmex* (1)	*Azteca* (4) *Tapinoma* (1) *Conomyrma* (1)	*Zacryptocerus* (1) *Pheidole* (3) *Crematogaster* (2) *Solenopsis* (1) *Leptothorax* (1) *Ochetomyrmex* (1) *Wasmannia* (1)	*Acanthoponera* (1) *Pachycondyla* (1) *Ectatomma* (1)	*Pseudomyrmex* (2)	17 (34)	Oliveira & Brandão (1991)
Ouratea hexasperma (Brasília, DF)	*Camponotus* (11)	*Azteca* (2)	*Zacryptocerus* (13) *Cephalotes* (1) *Pheidole* (2) *Crematogaster* (2)	*Pachycondyla* (1)	*Pseudomyrmex* (2)	8 (24)	Oliveira et al. (1995)
Qualea grandiflora (Itirapina, SP)	*Camponotus* (4) Unidentified genus(1)	Unidentified genus(1)	*Zacryptocerus* (2) *Wasmannia* (1)	*Ectatomma* (1)	*Pseudomyrmex* (2)	7 (12)	Oliveira et al. (1987)

needed in order to demonstrate that visitation by ants would in fact reduce herbivore damage to *Q. grandiflora*. A second field experiment with trees of *Q. grandiflora* was carried out to test this hypothesis.

Costa *et al*. (1992) compared the levels of herbivore damage to leaves of 15 pairs of experimental *Q. grandiflora* trees. An experimental plant pair consisted of two neighbouring *Q. grandiflora* trees, each being randomly assigned as either a control or treatment plant. Ants had free access to control plants but were impeded from climbing onto treatment *Q. grandiflora* trees by the application of a sticky barrier to the base of their trunks (15 cm above ground). Results showed that, after two months of exposure to herbivores, ant-excluded trees suffered significantly higher levels of leaf damage by *Compsolechia* caterpillars (Lepidoptera: Gelechiidae) than ant-visited control plants (Costa et al. 1992). Field observations indicated that foraging ants visiting *Qualea*'s EFNs did in fact attack the caterpillars on the leaves of control plants.

It remained to Del-Claro *et al*. (1996) to unequivocally demonstrate that ant visitation to *Qualea* can increase plant fitness in the cerrado by limiting herbivore damage to leaves, buds and flowers of *Q. multiflora*. These authors showed that herbivore deterrence by visiting ants increases in 40% the fruit set of control *Q. multiflora* trees as compared to ant-excluded trees.

Experiments with *Caryocar brasiliense* (Caryocaraceae). *Caryocar brasiliense* is a typical plant of the Brazilian cerrados, locally known as "pequizeiro" through most of its distribution. The plant has EFNs on the outer surface of the bud sepals and at the margins of shoot tips (Oliveira & Leitão-Filho 1987). Systematic censuses of the associated ant fauna (see above) revealed that the plant is actively visited by ants both day and night (Oliveira & Brandão 1991). Results from a 3-year study in the cerrado area of Itirapina (São Paulo) revealed that ant visitation to EFNs of *C. brasiliense* can markedly affect the infestation levels by most of the principal

insect herbivores of the plant (Oliveira 1997).

Shrubs of *C. brasiliense* are more frequently visited by ants than neighbouring plants without EFNs. Moreover, visiting ants attack and remove live insects which they find on the plant's foliage, especially near the EFNs. The results of the ant-exclusion experiments with *Caryocar* shrubs are summarized below for five principal associated herbivores (see also Oliveira 1997):

Eunica bechina Talbot (Lepidoptera: Nymphalidae) - eggs are laid singly on young leaves and shoot tips, and the larvae feed preferentially on young leaves (Oliveira & Freitas 1991; Freitas & Oliveira 1992). Foraging ants do not destroy *Eunica* eggs, but may prey and remove the caterpillars from the plant. Ant-excluded plants are significantly more infested by eggs and larvae of *E. bechina*, and adult butterflies visually avoid ovipositing on plants with high levels of ant visitation (Freitas & Oliveira 1996);

Edessa rufomarginata (De Geer) (Hemiptera: Pentatomidae) - adults mate on the plant, and egg batches consist of 6-14 eggs. Nymphs and adults feed on buds and fruits. Foraging ants prey on nymphs, and disturb nymphs and adults when these are feeding or walking on the plant. Plants without ants have increased numbers of hemipteran eggs;

Prodiplosis floricola (Felt) (Diptera: Cecidomyiidae) - females oviposit on developing buds which are destroyed by the larvae. High ant densities near the EFNs disturb ovipositing flies. Ant-excluded inflorescences have a significantly greater proportion of buds infested by the dipterans as compared to inflorescences with free ant access;

Unidentified stem-galling wasp (Hymenoptera: Chalcidoidea) - wasps induce galls on the stem. Heavily attacked branches are deprived of leaves and reproductive organs. Intense ant traffic along the stem, which is the main route to the EFNs, probably disturbs ovipositing wasps. Ant-excluded plants had higher infestation levels by stem-galling wasps;

Unidentified leaf-galling wasp (Hymenoptera: Chalcidoidea) - wasps induce galls over
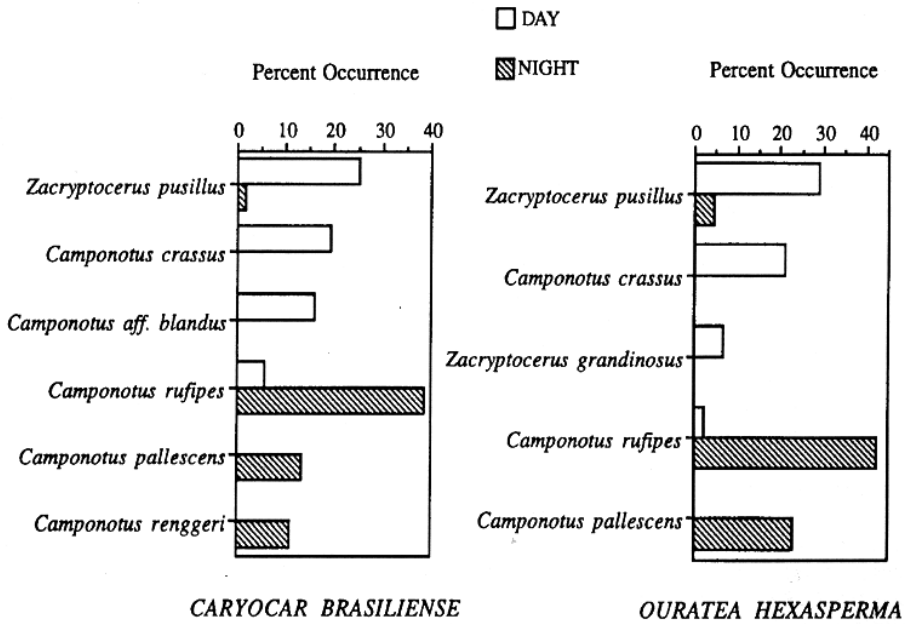
Figure 1. Daily turnover in species compositon of the principal ant visitors to the extrafloral nectaries of *Caryocar brasiliense* (left) in a cerrado area of Itirapina (SP), and *Ouratea hexasperma* (right) in a cerrado area near Brasília (DF). A total of 27 ant species were recorded during censuses on *Caryocar*, and 24 on *Ouratea*. Data are expressed as the percent occurrence of each species during diurnal and nocturnal censuses on each plant species. See also Oliveira & Brandão (1991) and Oliveira *et al*. (1995).

the leaf blade. Heavily attacked leaves fall prematurely. Ants have no effect on the infestation levels by leaf-galling wasps.

The experimental study with *C. brasiliense* demonstrated that ant visitation to EFNs significantly decreases the infestation levels by four out of five of the principal herbivores associated with this cerrado plant species. However, as opposed to the findings of Del-Claro *et al*. (1996) with *Qualea multiflora* (see above), such a deterrent effect by the ants does not affect the reproductive output of *C. brasiliense*. Although flower and initial fruit production was significantly greater on ant-visited than on ant-excluded shrubs of *Caryocar*, higher abortion rates of initial fruits by ant-visited plants resulted in similar final fruit and seed sets for both categories of ex-

perimental plants (Oliveira 1997).

Contrary to *Qualea multiflora* trees which produce many dry 'cheap' fruits with 10 to 18 wind-dispersed seeds (Del-Claro *et al*. 1996), *C. brasiliense* shrubs produce 1 to 4 fleshy 'expensive' fruits containing 1 to 4 large vertebrate-dispersed seeds (Gottsberger & Silberbauer-Gottsberger 1983). Since cerrado soils are characteristically poor (Eiten 1972) and the lack of soil nutrients is known to negatively affect final fruit set in plants (Stephenson 1981), it is reasonable to suppose that the low fertility of cerrado soils could constrain the ability of *Caryocar* shrubs to provide the resources necessary for growth and development of their heavy fleshy fruits. Competition among developing fruits and subsequent abortion would therefore neutra-

lize the initial higher production of flowers and fruits by ant-visited *Caryocar* shrubs as compared to ant-excluded ones (Oliveira 1997). Although this hypothesis needs further confirmation with soil-enrichment experiments (see Willson & Price 1980), resource limitation has already been suggested to affect other ant-plant systems (Kelly 1986, Folgarait & Davidson 1994).

Finally, although herbivore deterrence by visiting ants does not affect the reproductive output of *Caryocar* shrubs in the cerrado, ant visitation to EFNs may still be advantageous for the plants if (see Oliveira 1987): (1) the ants protect the plant's vegetative tissues during plant growth; (2) the plant's attractiveness to bat pollinators is increased by a large floral display (Augspurger 1980, Gribel & Hay 1993); (3) a surplus number of hermaphroditic flowers increases male contribution to fitness through pollen donation (Willson & Price 1977); (4) a surplus number of initial fruits and seeds allows the plant to selectively abort genetically inferior progeny (Janzen 1977).

Ant Foraging on Extrafloral Nectaries and its Effects on the Behavioral Biology of Insect Herbivores

Ants comprise an important component of the insect fauna found on the plant surface, especially on plant species producing food rewards such as extrafloral nectar (Oliveira & Brandão 1991). As we have seen, herbivore deterrence on such plants results from the ants' predatory and/or aggressive behavior near the nectar source (Bentley 1977). Phytophagous insects exploiting ant-visited plants must cope with the threat of ant predation or ant-induced injuries, and many of such herbivore species have developed an array of mechanisms to circumvent the ants' deterring capacities on their host plants (Janzen 1967, Koptur 1984, Heads & Lawton 1985, Costa *et al.* 1992). One of these mechanisms involve the secretion by the insect herbivore of sweet appeasing substances which decrease the risk of ant attacks on the host plant, as for exam-

ple in some ant-tended homopterans and butterfly larvae (Mallicky 1971, Atsatt 1981, Buckley 1987, Del-Claro & Oliveira 1996).

Most experimental studies on the interaction between ants and EFN-bearing plants have focused on the protective role of the ants against the plant's associated herbivores and the consequences of such protection, if any, on the plant's reproductive output (reviewed by Koptur 1992). It is surprising that such ant-plant systems have rarely been studied from the herbivore's standpoint (but see Heads & Lawton 1985). Although a few studies have already examined the effects of ant interference on butterfly biology and behavior, most of the data is descriptive rather than experimental (Brown 1981, Turner 1981, Smiley 1985, 1986).

Recent field experiments with the butterfly *E. bechina* on shrubs of *C. brasiliense* investigated how ant visitation patterns to this nectary plant can affect the behavioral biology of both immature and adult *Eunica*. Results can be summarized as follows (see also Freitas & Oliveira 1992, 1996): *Eunica* caterpillars feed on young leaves of *Caryocar* and larval mortality is strongly dependent on the level of ant visitation to the host plant. Larvae feeding on highly visited plants have an increased risk of ant predation. Vulnerability to ant predation, however, decreases with larval size. Stick-like frass chains constructed by the larvae at leaf margins were demonstrated to be a safe refuge against attacks by foraging ants on *Caryocar*. Butterfly eggs are not removed by ants, but the oviposition behavior of *Eunica* is strongly affected by the level ant visitation to the plants. *Eunica* females visually avoid ovipositing on highly visited plant locations — branches with artificial rubber ants were less infested by butterfly eggs than control branches with rubber circles. These data show that ant visitation patterns on *Caryocar* shrubs strongly affect the behavior of both immature and adult *Eunica*, and provide the first demonstration that egg-laying decisions by a non-myrmecophilous butterfly can be influenced by ant presence on the host plant (see also

Attsat 1981, Pierce & Elgar 1985, Freitas & Oliveira 1992, 1996, Oliveira 1997).

Concluding Remarks

Plants bearing extrafloral nectaries are widespread amongst the woody flora of Brazilian cerrado vegetation. A diverse assemblage of nectar-gathering ant species visit these glands both day and night and may act as anti-herbivore agents, significantly reducing herbivore damage on vegetative as well as on reproductive plant parts. The outcome of such facultative mutualistic associations, however, may vary both geographically and temporally and may be also conditioned by diverse factors such as the species of visiting ant and the escape tactics of the associated herbivore species (Koptur 1992, and included references). Future research on ants and EFN-bearing plants in cerrado vegetation should take into account other factors that may possibly also affect ant-derived benefits to the plants . For example, the degree to which herbivore deterrence by ants can be translated into greater fecundity (i.e., increased number of fruits and seeds) by a given nectary plant species may vary with traits such as the plant's habit (shrub *versus* tree) and fruit type (dry *versus* fleshy fruits), as well as with soil nutrients. Although there is evidence suggesting that such factors may condition the outcome of certain ant-plant systems in the cerrado (Del-Claro *et al.* 1996, Oliveira 1997), additional experiments are needed in order to better understand the dynamics of such mutualistic interactions in this vegetation type.

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