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15

Ant Foraging on Plant Foliage: Contrasting Effects on the Behavioral Ecology of Insect Herbivores

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ANTS ARE DOMINANT ORGANISMS WHOSE INDIVIDUAL COLONIES may contain several million workers. Their numerical dominance in terrestrial habitats is combined with a broad taxonomic diversity and a widespread distribution throughout the Globe (Hölldobler and Wilson 1990). The ecological success of ants is attributed to their eusocial mode of life, local abundance, and diversity of adaptations, among other things (Wilson 1987). Such traits result in a wide variety of feeding habits and foraging strategies, including the use of plant foliage as a foraging substrate (Carroll and Janzen 1973). Intense foraging on vegetation appears to have set the scenario for a multitude of interactions with many plant species worldwide, ranging from facultative to obligate ant-plant associations (reviewed by Davidson and McKey 1993; Bronstein 1998). Incidentally, by frequently foraging on the plant surface, ants often affect the life of a particular trophic group: the herbivores.

Why are ants so common on foliage? First, ants may nest in plant structures, and therefore the plant itself is part of the colony's immediate patrolled area (Janzen 1967). Second, ground-nesting ants may extend their foraging areas by climbing on plants to search for food (Carroll and Janzen 1973). A predictable food source can reinforce ant visitation to a particular plant location, and plant-derived food products such as extrafloral nectar and/or food bodies are known to promote ant activity on foliage (Bentley 1977; Koptur 1992). Additionally, some insect herbivores may also produce food secretions that are highly attractive to a variety of ant species (Way 1963; Malicky 1970; DeVries and Baker 1989).

Whatever the factor promoting their activity on plants, ants may affect the life of insect herbivores in different ways, resulting in positive, negative, or neutral consequences (Bronstein 1994). Most studies on ant-plant interactions, however, have focused on the deterrence of insect herbivores by ants and the possible influence of such activity on plant fitness (Bronstein 1998, and included references). Rarely has this interface been studied from the herbivore's standpoint (Heads and Lawton 1985). In this chapter we illustrate how intense ant activity on plant foliage can strongly affect the behavioral ecology of insect herbivores in the cerrado. We first present the factors that likely promote ant foraging on cerrado plants, and then describe two case studies that demonstrate a close link between the behavior of insect herbivores and their encounters with ants on the plant surface.

ANT FORAGING ON CERRADO PLANTS

Several factors contribute to the ubiquity of ants on cerrado plant foliage. First, the stems of many plants are hollowed out by boring beetles, and the galleries are then used as nesting sites by numerous arboreal ant species. Morais (1980) recorded a total of 204 arboreal ant colonies in 1,075 m^2 of *campo cerrado* (scattered shrubs and trees; see chapter 6), and within this area 136 live woody individuals and 17 dead standing trunks were found to house stem-nesting ants. Such a high occurrence of ant nests in the vegetation likely results in intensive foraging on cerrado foliage (Morais 1980; Morais and Benson 1988) and rivals similar censuses undertaken in tropical forests (Carroll 1979). Second, plants bearing extrafloral nectaries are abundant among local woody floras (Oliveira and Leitão-Filho 1987; Oliveira and Oliveira-Filho 1991; Oliveira and Pie 1998), and such glands have been shown to be important promoters of ant activity on the cerrado foliage (see fig. 15.1A, B; see also Oliveira et al. 1987, Oliveira and Brandão 1991; Costa et al. 1992; Oliveira et al. 1995). Third, insect herbivores that produce food secretions play a key role in attracting ants to leaves, and both honeydew-producing homopterans and lycaenid butterfly larvae are known to induce ant foraging on cerrado plants (fig. 15.1C, D; Dansa and Rocha 1992; Lopes 1995; Del-Claro and Oliveira 1996, 1999; Diniz and Morais 1997).

Given that ants are dominant components of the insect fauna found on the cerrado foliage, experimental investigation of ant-herbivore inter-

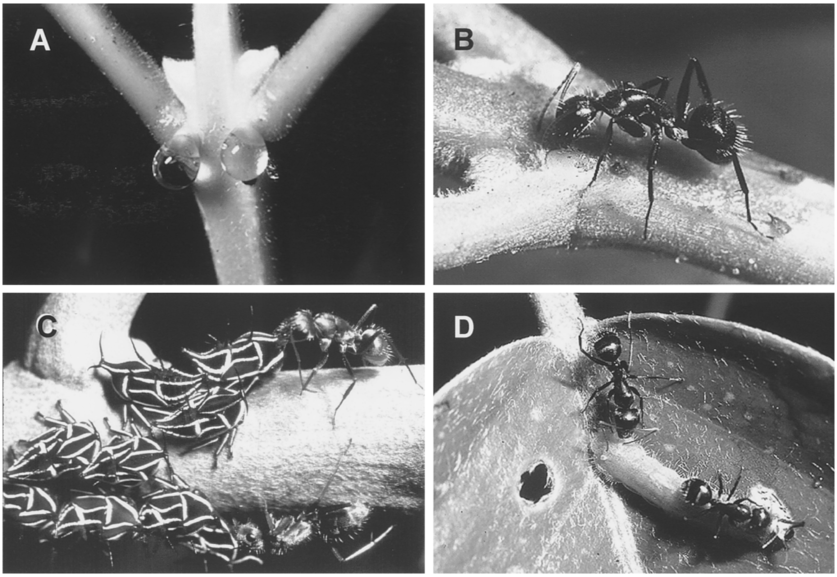

Figure 15.1 Liquid food sources for ants on cerrado foliage. (A) Accumulated extrafloral nectar in *Qualea grandiflora* (Vochysiaceae). (B) *Camponotus* sp. collecting extrafloral nectar at *Q. grandiflora*. (C) *Camponotus blandus* collecting honeydew from a *Guayaquila xiphias* treehopper. (D) *Synargis* (Riodininae) caterpillar being tended by *Camponotus* ants.

actions in this vegetation type should be particularly profitable for testing hypotheses concerning the impact of ants on herbivore survival and behavior. Recent experimental work with two distinct systems has provided strong evidence that the occurrence of ant-herbivore encounters on the host plant can be largely mediated by behavioral patterns of the herbivore. Results show that, depending on the nature of the impact of the ants (negative or positive), herbivore behavior can promote either the breakage or the reinforcement of the relationship, thereby decreasing or increasing the chance of encountering an ant on the host plant (see fig. 15.2).

ANT-BUTTERFLY INTERACTIONS

Ant effects on butterfly biology and behavior have been investigated for decades, with most studies focusing on myrmecophilous lycaenid species whose larvae are protected against natural enemies by tending ants (Malicky 1970; Pierce and Mead 1981; Pierce and Elgar 1985; DeVries 1984, 1991). By living in close proximity to ants, however, butterfly larvae risk

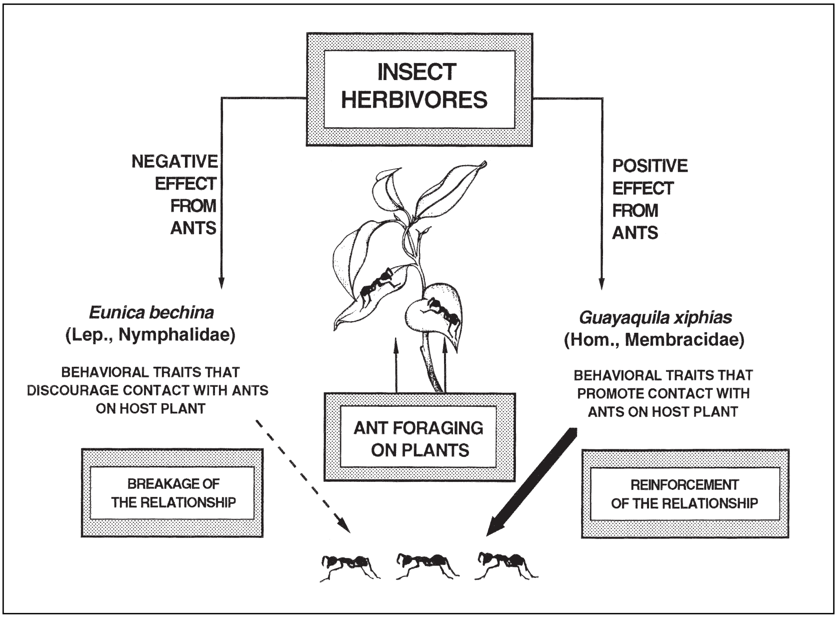

Figure 15.2 Diagram illustrating how behavioral traits of insect herbivores can mediate contact with ants on the host plant. Depending on the nature of the impact from foraging ants—negative or positive—herbivores can mediate the interaction either by avoiding (*Eunica* butterflies) or promoting (*Guayaquila* treehoppers) contact with ants on the host plant.

attack by the latter (but see DeVries 1991). This risk is minimized/avoided by lycaenid larvae via traits that decrease physical damage from ant attacks, reduce ant aggressiveness, and/or incite tending behavior. Such traits include a protective thick cuticle, the production of sweet appeasing substances, ant-mimicking vibration calls, and reduction of the beat reflex upon disturbance (Malicky 1970; DeVries 1990, 1991). The energetic costs to lycaenid larvae of feeding associated ants may include a prolongation of larval development (Robbins 1991) and a sex-related loss of pupal weight (Fiedler and Hölldobler 1992). However, no measurable cost to larvae has been found in other ant-lycaenid systems (DeVries and Baker l989; Cushman et al. 1994; Wagner and Martinez del Rio, 1997).

On the other hand, larvae of non-myrmecophilous butterflies are frequently preyed upon or removed from host plants by foraging ants (Jones 1987; Freitas and Oliveira 1992, 1996; Freitas 1999). Caterpillars of many lepidopteran species have evolved traits to escape ant predation, especially on ant-visited plants (reviewed by Heads and Lawton 1985; Salazar and Whitman 2001). Few studies, however, have been conducted on these systems, and most were with *Heliconius* butterflies (Benson et al. 1976; Smiley 1985, 1986). To date only one ant-butterfly system has been documented in greater detail in the cerrado (Freitas and Oliveira 1992, 1996; Oliveira 1997). We here summarize the negative effects of ants on a non-myrmecophilous butterfly, *Eunica bechina*, and show that both the larval and adult stages possess traits that result in decreased contact with ants on a highly ant-visited host plant (fig. 15.2).

Negative Impact of Ants: Eunica *Butterflies vs. Ants on a Nectary Plant*

Eunica bechina (Nymphalidae) is a non-myrmecophilous butterfly whose larvae feed on *Caryocar brasiliense* (Caryocaraceae). This host plant bears extrafloral nectaries on the sepals and leaf buds, and is visited day and night by 34 species of nectar-gathering ants in an area of cerrado *sensu stricto* (see chapter 6) near Itirapina, SE Brazil (Oliveira and Brandão 1991). Controlled ant-exclusion experiments revealed that visiting ants decrease the infestation levels of three common herbivores of *Caryocar*, including eggs and larvae of *E. bechina* (see Oliveira 1997).

Females lay eggs singly on young leaves, on which the caterpillars preferably feed (Oliveira and Freitas 1991). As also recorded for a number of other nymphalids (DeVries 1987), *Eunica* larvae rest on stick-like frass chains constructed at leaf margins (see fig. 15.3B). A series of field observations and experiments on the system involving *Eunica* and ants (Freitas and Oliveira 1992, 1996) has demonstrated that the behavioral biology of the butterfly is closely linked with ant activity on the host plant, and can be summarized as follows.

Ants and butterfly eggs. Although ants are known to prey on or remove insect eggs from plants (Letourneau 1983), they do not consume or remove *Eunica bechina* eggs from the host plant (Freitas and Oliveira 1996). Field observations indicated that foraging ants frequently walk in the vicinity of *Eunica* eggs but ignore them. On plants other than *Caryocar*, we have observed *Pheidole* ants preying on eggs of the nymphalid butterflies *Actinote pellenea* and *Dione juno*, whereas *Crematogaster* ants prey on eggs of *Placidula euryanassa*. Both *Pheidole* and *Crematogaster* also consume eggs of *Anaea otrere* (J. M. Queiroz and P. S. Oliveira, unpublished data). Such butterfly eggs (all non-euryteline Nymphalidae) consumed by foraging ants have a soft chorion and are weakly attached to the host plants. Features like toughness and firm attachment to leaves possibly account for the lack of attractiveness of *Eunica* eggs to the ants that forage on *Caryocar*.

Ant activity and caterpillars. Foraging ants frequently found and

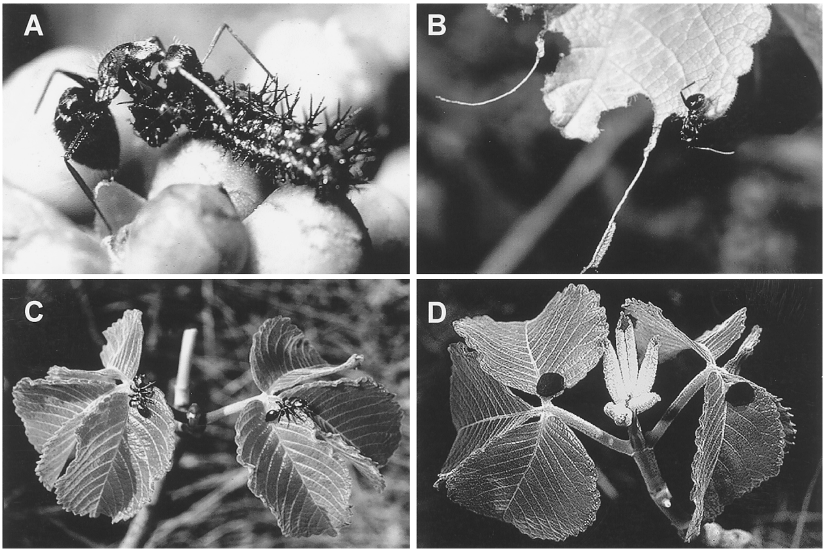

Figure 15.3 Interaction between *Eunica bechina* and ants. (A) *Camponotus* sp. attacking a third-instar caterpillar. (B) Second-instar caterpillar resting motionless on the tip of its stick-like frass chain, as a *Camponotus* ant forages nearby. Note a previously used frass chain at upper left. (C) Rubber ants and (D) control rubber circles used in field experiments to test whether adult *Eunica* visually avoid ovipositing on ant-occupied plant locations. See also fig. 15.4.

attacked *Eunica* caterpillars on the host plant (fig. 15.3A), and field experiments revealed that larval mortality is affected by the rate of ant visitation to the host plant (see fig. 15.4C). Larval vulnerability to ant predation, however, varies with the ant species and size of the caterpillar (Freitas and Oliveira 1992, 1996). If touched by ants, larvae usually display the beat reflex (curling and wriggling; see Malicky 1970) and/or also jump off the leaf and hang by a silken thread. When an ant bites a caterpillar, the latter vigorously bends its body towards the ant and frequently regurgitates, eventually inhibiting further ant attacks. Moreover, field experiments have demonstrated that the stick-like frass chains built by caterpillars at leaf margins (fig. 15.3B) constitute a safe refuge against ant predation on the host plant (fig. 15.4D). Although frass chains have long been described by naturalists, and their function has been assumed to be predator avoidance (DeVries 1987, and included references), the field experiment on ant-*Eunica* interactions demonstrated their relevance for larval survival on a host plant with high rates of ant visitation.

Ant activity and ovipositing females. Female butterflies avoid

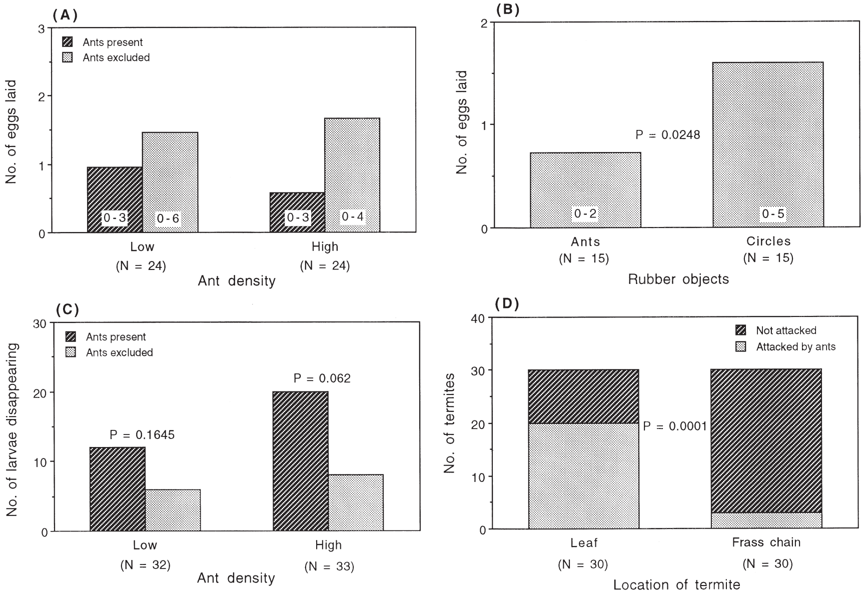

Figure 15.4 Field experiments on the interaction between *Eunica bechina* and ants on shrubs of *Caryocar brasiliense*. (A) Oviposition by *Eunica* females on egg-free experimental branch pairs during a 24 h period. Ant presence negatively affects butterfly oviposition, but the effect is significant only under high rates of ant visitation (mean > 0.5 ants per branch in six previous censuses). (Mann-Whitney *U*-tests; ranges are given inside bars). (B) In 2-choice experiments using egg-free plants, butterflies laid more eggs (after 24 hours) on plant branches bearing rubber circles than on neighboring branches with rubber ants (Mann-Whitney *U*-tests; ranges are given inside bars). (C) Ant foraging negatively affects caterpillar survival on the host plant, but mortality after 24 hours is significant only on branches with high ant density (*G* tests). (D) During 10-min trials, foraging ants attack live termites in significantly greater numbers on *Caryocar* leaves than on the frass chains constructed by *Eunica* caterpillars (*G* tests). (After Freitas and Oliveira 1996). See also fig. 15.3.

ovipositing on plant locations with high ant densities (fig. 15.4A). Although chasing by ants can have an inhibitory effect on the oviposition behavior of female insects (Janzen 1967; Schemske 1980), this was not detected in our observations of *E. bechina*. Since ants do not chase egg-laying *Eunica*, and the oviposition event lasts only 1–3 seconds, the differential occurrence of butterfly eggs on ant-visited and ant-excluded *Caryocar* plants (Oliveira 1997) presumably results from the discriminating abilities of the ovipositing female. This hypothesis was tested by simultaneously placing artificial rubber ants and rubber circles at neighboring branches of the host plant (fig. 15.3C, D). The results unequivocally indicate that branches with rubber ants were less infested than those with rubber circles (fig. 15.4B) and that visual cues (i.e., ants) likely mediated egg-laying decisions by the butterfly. Although ant presence *per se* was shown to produce an avoidance response by *E. bechina* females, ant behavior and/or chemical cues could also potentially affect female oviposition.

In conclusion, *E. bechina,* in both immature and adult life stages, possesses traits that facilitate living in an ant-rich environment. Although such traits are probably more clear-cut in the larvae (i.e., jumping off the leaf, construction of frass chains) than in the adults (selection of plants with low ant densities), the correct decision of the egg-laying female can be crucial for the survival chances of her offspring.

Ants can inhibit herbivore occupation of host plants and have been thought to provide a consistent defense system relatively immune to evolutionary changes by the herbivore (Schemske, 1980). One may expect that lepidopteran larvae bearing ant-avoiding traits would have an advantage in the cerrado ant-rich environment. Even if larvae-constructed frass chains did not evolve as a direct response to the risk of ant predation, they may have initially facilitated the use of ant-visited plants by increasing larval safety against ant attacks. Data from field experiments strongly suggest that such stick-like structures at leaf margins provide protection against walking predators (Freitas and Oliveira 1996; Machado and Freitas 2001).

Butterflies are known to use visual cues prior to oviposition to evaluate both plant quality and the presence of conspecific competitors (Rausher 1978; Williams and Gilbert 1981; Shapiro 1981). The field study of *Eunica bechina* demonstrated that visual detection of ant presence can also mediate egg-laying decision by female butterflies (Freitas and Oliveira 1996). Although the influence of ants on oviposition decisions of butterflies has been documented in species with myrmecophilous larvae (Pierce and Elgar 1985), the precise cues eliciting the oviposition response have never been determined. Although our work has shown that visual detection of ant presence can inhibit butterfly oviposition, there is likely an array of ant-avoiding traits still to be discovered.

ANT-HOMOPTERA INTERACTIONS

The honeydew produced by phloem-feeding Homoptera (primarily aphids, membracids, and scales) is an ant attractant consisting of a mixture of sugars, amino acids, amides, and proteins (Auclair 1963). Associations between ants and such homopteran groups have been commonly considered mutualistic (Way 1963). Tending ants may harvest the energy-rich fluid around the clock (fig. 15.1C) and in turn provide a range of benefits to the homopterans, including protection from predators and parasitoids, and increased fecundity (Bristow 1983; Buckley 1987). Honeydew can be a relevant item in the diet of many ant species (Tobin 1994; Del-Claro and Oliveira 1999), and intra- and interspecific competition among homopteran aggregations for the services of ants can negatively affect homopteran fitness through reduced tending levels (Cushman and Whitham 1991). Ant-derived benefits to honeydew-producing Homoptera can also vary with factors such as the species of ant partner, size of homopteran group, developmental stage of homopterans, frequency of ant attendance, and predator abundance (Cushman and Whitham 1989; Breton and Addicott 1992; Del-Claro and Oliveira 2000; Queiroz and Oliveira 2000). Therefore, the outcomes of ant-homopteran associations are strongly dependent upon the ecological conditions in which they occur (Cushman and Addicott 1991; Bronstein 1994).

Although experimental research on ant-plant-homopteran interactions has increased markedly over the past two decades, most studies come from temperate areas (e.g., Bristow 1983, 1984; Buckley 1987; Cushman and Whitham 1989, 1991). Only recently have these associations been studied in tropical habitats, including the Brazilian cerrados (Dansa and Rocha 1992; Del-Claro and Oliveira 1999, 2000). We report here on the system involving the treehopper *Guayaquila xiphias* (Membracidae) and ants, and show that ant-tending can positively affect both homopteran survival and fecundity, and that the homopterans' capacity to attract ants early in life is a crucial behavioral trait reinforcing this relationship (fig. 15.2).

Positive Impact of Ants: Guayaquila *Treehoppers and Honeydew-Gathering Ants*

The honeydew-producing treehopper *Guayaquila xiphias* feeds on shrubs of *Didymopanax vinosum* (Araliaceae) in the cerrado vegetation (*sensu stricto*, see chapter 6) near Mogi-Guaçu, SE Brazil, and occurs in aggregations of 1 to 212 individuals near the flowers or the apical meristem (see fig. 15.5A, C; Del-Claro and Oliveira 1999). *Guayaquila* females exhibit parental care and guard both the egg mass and young nymphs (fig. 15.5A, B). Nymphs develop into adults in 20–23 days, and then disperse from the natal aggregations. Treehopper aggregations are tended day and

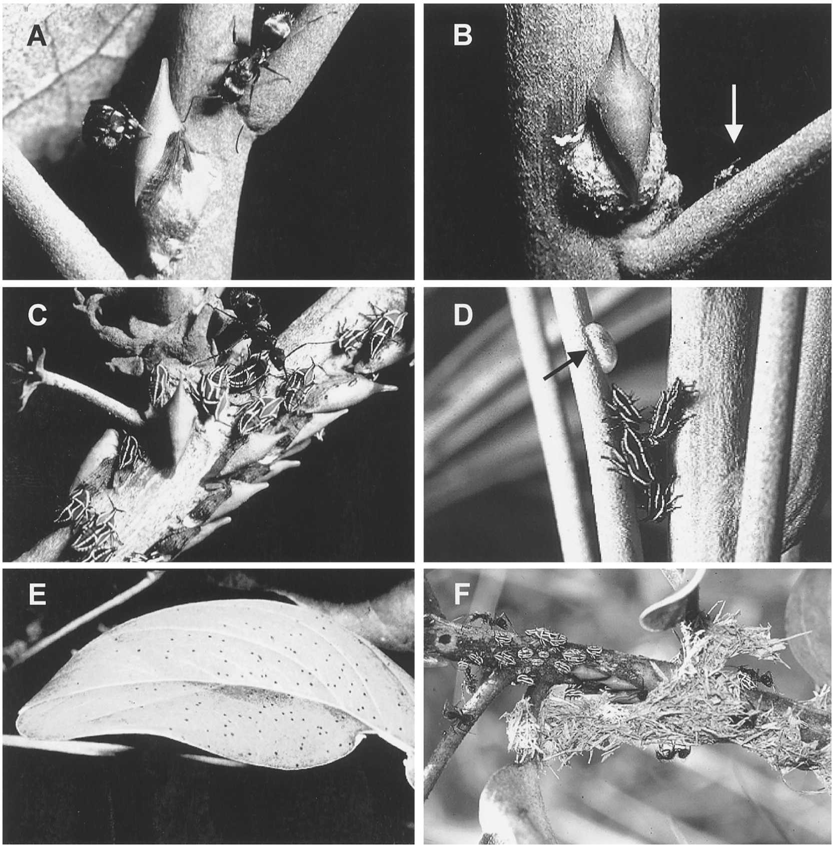

Figure 15.5 Interaction between ants and honeydew-producing *Guayaquila xiphias* treehoppers. (A) Brood-guarding *Guayaquila* female being tended by *Camponotus blandus* ants. (B) *Gonatocerus* parasitoid wasp (arrow) near an untended brood-guarding female. (C) *Camponotus rufipes* tending a *Guayaquila* aggregation. (D) Larvae of predatory *Ocyptamus* syrphid fly (arrow) near untended treehopper nymphs. (E) Scattered droplets of flicked honeydew on leaves beneath an untended *Guayaquila* aggregation. (F) Ant-constructed shelter for *Guayaquila*. See also fig. 15.6.

night by an assemblage of 21 honeydew-gathering ant species, which may construct shelters as satellite nests to house the homopterans (fig. 15.5F; Del-Claro and Oliveira 1999). The attractiveness of *Guayaquila*'s honeydew to ants is high enough to maintain tending activities unchanged, even after the ants have discovered an alternate sugar source on the host plant (Del-Claro and Oliveira 1993).

A series of field observations and controlled experiments has revealed that the treehoppers can receive a range of benefits from ant-tending and that their behavior can promote contact with ants on the host plant (Del-Claro and Oliveira 1996, 2000). The ecology of the system can be summarized as follows.

Ant effects on Guayaquila*'s natural enemies.* Due to continuous honeydew-gathering activity, ant density at any given time is higher near the treehoppers than at other plant locations, and this can markedly affect the spatial distribution and foraging behavior of *Guayaquila*'s natural enemies, such as parasitoid wasps, salticid spiders, and syrphid flies (fig. 15.5B, D). For instance, parasitoid distribution on the plant was shown to be significantly affected by increased ant activity near brood-guarding *Guayaquila*, and parasitization of treehopper ovipositions was more successful in the absence of ants (fig. 15.5A, B; Del-Claro and Oliveira 2000). Aggressive toward intruding predators and parasitoids, tending ants not only ward off such enemies from the vicinity of the treehoppers, but may also attack and kill the intruders. Controlled ant-exclusion experiments revealed that ant presence decreases the abundance of *Guayaquila*'s natural enemies on the host plant (see fig. 15.6A).

Ant-derived benefits to Guayaquila xiphias. Ant-exclusion experiments have demonstrated that tending ants can have a positive impact on treehopper survival (fig. 15.6 B). Moreover, ants can also confer a direct reproductive benefit to *Guayaquila* (see also Wood 1977; Bristow 1983). By transferring parental care to ants, ant-tended brood-guarding females (fig. 15.5A) have a higher chance of producing an additional clutch than untended females (91% *vs.* 54% of the cases; $P = 0.018$, $\chi^2 = 5.61$; $N = 22$ females in each experimental group). Two years of experimental manipulations, however, have shown that ant-derived benefits related to protection and fecundity can vary with time and/or with the species of tending ant (Del-Claro and Oliveira 2000). Several other studies have also shown that species of ants may differ greatly in the protection they afford to homopterans, and this may depend on the ants species-specific traits such as size, promptness to attack intruders, morphological and chemical weapons, as well as recruitment behavior (e.g., Addicott 1979; Messina 1981; Buckley 1987; Buckley and Gullan 1991).

Attraction of ants through honeydew flicking. Ant-tending unequivocally plays a crucial role in the survival of developing brood of *Guayaquila xiphias* in the cerrado, as also shown for other temperate ant-membracid systems (e.g., Bristow 1983; Cushman and Whitham 1989). It is therefore reasonable to predict that any behavior promoting early contact with ants would be advantageous for ant-tended treehoppers (see also DeVries 1990; DeVries and Baker 1989, on ant-tended caterpillars). *Guayaquila xiphias* females, as well as developing nymphs, frequently flick away the accumulated honeydew if it is not promptly collected by

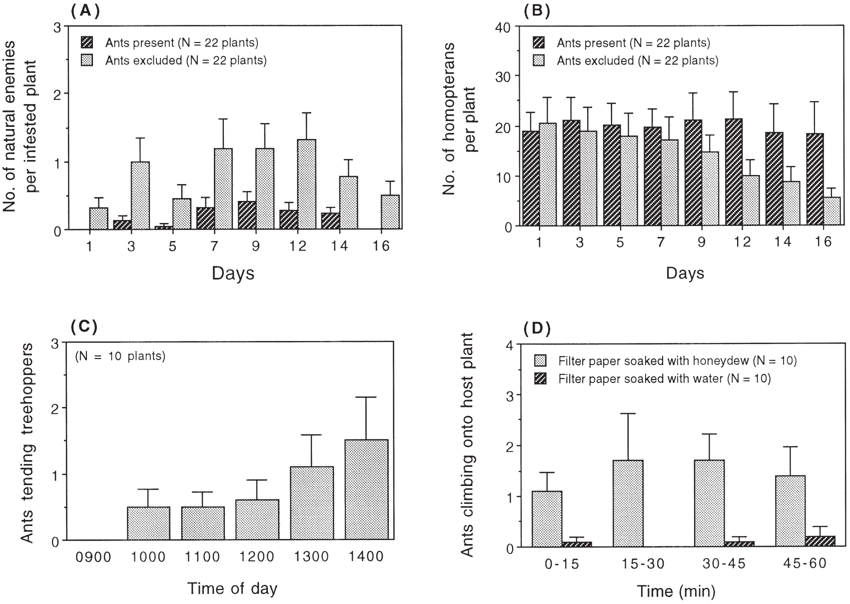

Figure 15.6 Field experiments on the interaction between honeydew-producing *Guayaquila xiphias* and tending ants on shrubs of *Didymopanax vinosum*. (A) Ant presence significantly reduces the number of *Guayaquila*'s natural enemies (spiders, syrphid flies, and parasitoid wasps) on the host plant (Treatment: $F = 11.54$, $df = 1$, $P = .0015$). (B) Ant-tending positively affects treehopper survival through time (Treatment × Time: $F = 4.33$, $df = 7$, $P = .0001$). (C) After finding scattered droplets of flicked honeydew on the ground beneath untended treehoppers, the number of ants involved with tending activities increases with time due to recruitment behavior ($F = 2.44$, $df = 5$, $P = .04$). (D) Pieces of honeydew-soaked filter paper placed beneath treehopper-free plants induce significantly more ground-dwelling ants to climb onto the plant than control papers with water (Treatment: $F = 15.89$, $df = 1$, $P = .001$). All tests performed with repeated-measures ANOVA. Data from (A) and (B) after Del-Claro and Oliveira (2000); (C) and (D) after Del-Claro and Oliveira (1996). See also fig. 15.5.

tending ants; this results in the occurrence of scattered honeydew droplets below untended or poorly tended treehopper aggregations (fig. 15.5E). Field experiments have shown that honeydew flicking by untended *Guayaquila* can provide cues to ground-dwelling ants, which climb onto the plant and start tending activities (fig. 15.6C, D; Del-Claro and Oliveira 1996). Groups of untended *Guayaquila* nymphs start secreting honeydew soon after introduction on previously unoccupied host plants.

Upon encountering the droplets on the ground, alerted ants climb onto the plant and eventually find the homopterans. The number of ants engaged in tending activities increases with time due to recruitment to the newly discovered food source (fig. 15.6C). Honeydew-soaked filter papers placed beneath unoccupied host plants further confirmed that flicked honeydew provides cues to ants and induces them to climb onto the plant (fig. 15.6D).

Attraction of Ants by Ant-Tended Insects

The presence of honeydew on lower foliage or on the ground beneath untended homopterans is well documented (Buckley 1987; Hölldobler and Wilson 1990). Douglas and Sudd (1980) discounted the possibility that scattered aphid honeydew attracted *Formica* ants since they had seen these ants ignoring fallen droplets. In the *Guayaquila*-ant association, however, we have shown that flicking accumulated honeydew can mediate this ant-homopteran system by promoting contact between potentially interacting species. Honeydew accumulated on the bodies or in the vicinity of untended homopterans may result in increased mortality due to fungal infections (Buckley 1987). It is therefore possible that ant attraction through honeydew flicking has evolved as a by-product of a primarily defensive behavior against fungi-induced damage.

Ant-tending may also confer a range of benefits to butterfly larvae in the family Lycaenidae (Pierce and Mead 1981; DeVries 1991). Some adult butterflies promote contact with ants by choosing ant-occupied plant individuals (Pierce and Elgar 1985). Myrmecophilous butterfly larvae and pupae produce substrate-borne vibrational calls, which have been demonstrated to attract nearby ants (DeVries 1990, 1992; Travassos and Pierce 2000). Therefore, for myrmecophilous butterflies, contact with tending ants can be promoted by both adults and immatures. Cocroft (1999) has recently shown that substrate-borne vibration calls are used in offspring-parent communication by *Umbonia* treehoppers. DeVries (1991b) has speculated that vibrational communication by ant-tended membracids as well as by other myrmecophilous insects could be used to maintain ant association.

CONCLUSIONS AND RESEARCH DIRECTIONS

Ant-plant-herbivore interactions offer numerous promising avenues for future research in the cerrado, with ramifications for different areas of experimental field biology and applied ecology. The uniqueness of the cerrado for this type of research relies on the prevalence of ants on the plant substrate, and on the abundance of predictable liquid food sources in the form of extrafloral nectar and insect-derived secretions. Moreover, arboreal ants commonly nest inside hollowed-out stems of cerrado plants (Morais 1980), and this per se promotes intense ant patrolling activity on leaves, regardless of the presence of liquid food rewards on the plant. The prevalence of ants on foliage makes ant-herbivore-plant interactions especially pervasive in the cerrado, as revealed by the high abundance of extrafloral nectary-mediated interactions (Oliveira and Oliveira-Filho 1991; Oliveira 1997), as well as the large number of ant-tended treehoppers (Lopes 1995) and lycaenids (Brown 1972) occurring in this biome. The data summarized in this chapter illustrate how foraging by ants on cerrado plants can affect herbivore biology in contrasting ways, and at the same time point to a number of facets in ant-herbivore systems that have not yet been investigated. For instance, although it is clear that both butterfly adults and larvae can either avoid (as in *Eunica*) or promote (as in ant-tended lycaenids) encounters with ants on the host plant, we are only beginning to understand the mechanisms through which such interactions can be behaviorally mediated by the herbivore. Although visual stimuli play an important role for *Eunica* females to avoid ants, the cues used by lycaenids to lay eggs on ant-occupied plants are still unknown. Similarly, we know virtually nothing of the decision mechanisms used by ant-tended treehoppers in selecting individual host plants. Is ant presence somehow perceived by treehopper females, and can this mediate oviposition? Can ant-tended treehoppers use vibrational communication to attract ant partners? Moreover, since the negative/positive impact of ants on a given herbivore species can vary among different ant species, can the herbivore tell ants apart and behave/respond differently to them depending on the intensity of their harmful/beneficial effects? Finally, the cerrado savanna is unique for the study of ant-plant-herbivore systems because in most cases the researcher can have full visual access to the foliage. Field work under this situation permits not only a more accurate description of the behavioral traits mediating the interactions, but also the development of controlled field experiments to identify the selective forces operating within such multitrophic systems.

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