

experimental demonstrations of ant protection, ants have been observed attacking insect herbivores.^{31,150,201,208,217}

In Nigeria, *Pachysima* ants occupy *Barteria* plants, resulting in more vegetative growth and less damage to shoot tips than in unoccupied plants.¹⁶⁸ The ants were observed to attack plants adjacent to their *Barteria* and to clean the large leaves of debris and epiphyllae, the first suggestion of the importance of "housekeeping" by ants benefitting the plants. Letourneau²²³ was the first to discover the importance of nonaggressive ants in plant protection: *Pheidole bicornis*, which are small and sluggish ants, were previously thought to function only in nutrient procurement of the myrmecophytic *Piper* spp. Her experiments demonstrated that the ants clean the surface of leaves from insect eggs and early instar larvae, thereby significantly reducing damage from foliage-feeding insects.

When studies have been conducted in sufficient detail, it is frequently revealed that some ant species are better than others in protecting plants. The eight ant species associated with *Calathea* differed greatly in the magnitude of their beneficial effects on seed production;¹⁵⁷ the smallest ants (*Wasmannia auropunctata*) were the best defenders, and plants with these ants set the greatest amount of seed (more than twice as much as plants defended by *Pheidole gouldi*). While the four species of ants commonly associated with *Inga densiflora* and *I. punctata* were all capable of removing some herbivores, *Pheidole biconstricta* was the most effective overall against all the major guilds of herbivores on the plants.²⁰¹ Of four ant species visiting extrafloral nectaries on reproductive structures of the orchid *Schomburgkia tibicinis*, the larger species (*Ectatomma tuberculatum* and *Camponotus rectangularis*) were best at reducing damage to inflorescences by beetles and thus increasing fruit set.²⁹⁹

Preliminary observations suggest that a loose association exists between the aggressive bullet ant *Paraponera clavata* and *Pentaclethra macroloba*:³⁰ the trees provide suitable nest sites for the ants and a food source in extrafloral nectar; the ants provide some amount of protection by collecting herbivorous insects. In some systems, ants protect plants against other ants. *Azteca* ants deter *Atta* defoliators from citrus trees in Trinidad.¹⁷⁵

7. Trade-Offs with Other Defenses

Once ant defense has been demonstrated, a related hypothesis is engendered: are there evolutionary trade-offs between ant defense and other types of antiherbivore defense? The diversion of resources from one type of defense to another may be termed a *trade-off*. Trade-offs could occur between types of defenses because plants have finite resources, and natural selection should act to optimize the pattern of resource allocation.⁷

A comparison of ant acacias and nonmyrmecophytic acacias revealed the species not protected by ants to have greater chemical protection,²⁹⁴ though not for all types of chemical defense (D. Seigler personal communication). Bentley³² observed that when *Bixa orellana* occur at higher elevations where ants are not abundant, the sepal nectaries are not evident and the sepals are much thicker, suggesting compensation for lack of ant defense with mechanical protection of ovules and developing seeds.

The bracken fern *Pteridium aquilinum* has nectaries that function primarily on developing fronds,^{271,336} providing potential ant protection of tender leaf tissue. Mature, fully hardened leaves do not have functional nectaries; perhaps mechanical defense makes ant protection less important. There is an obvious trade-off in chemical defenses as fronds age: young fronds have cyanogenic glycosides, whereas mature fronds have high levels of tannins.⁷¹

The same species of *Inga* that are protected by ants in the lowland wet forest occur at higher elevations without ant defense; higher elevation *Inga* have more phenolic compounds in their foliage than their lower elevation counterparts. Alternative defenses do not fully compensate for the lack of ant defense, however, as upland trees sustain more damage than lowland trees.²⁰²

A comparison of the defenses of *Ipomoea* species (potential chemical defense from indole alkaloids, potential biotic defense from nectaries, and potential mechanical defense from pubescence and woodiness) gave no evidence of trade-offs.³²⁹ Despite this negative result, it is certain that the generalized nature of ant defense is in some systems superior to any combination of alternative defenses.²⁰⁶

F. OTHER PREDATORS AND PARASITIDS FEEDING AT NECTARIES

The importance of extrafloral nectar in supporting predators (in addition to ants) is well documented for cultivated cotton.^{3,302,356} Many arthropod predator species are much more abundant on cotton with extrafloral nectaries than on nectarless cotton.¹ Lacewings and several coccinellid species were observed feeding at peach leaf nectaries.²⁹¹ Floral nectaries in wind-pollinated *Croton suberosus* function to attract *Polistes* wasp predators of the herbivores.⁹⁶ Overall, however, less work has been directed to nonant predators than to parasitoids supported by extrafloral nectaries.

Adult parasitoids require carbohydrates and water to achieve maximum longevity.¹²⁰ The short mouthparts of parasitic Hymenoptera limit their use of nectar to sources that are easily accessible, such as unspecialized flowers or extrafloral nectar.⁶⁴ Sixty species of Ichneumonidae fed at the extrafloral nectaries of faba bean, *Vicia faba*.⁶⁵

The foliar nectaries of *Byttneria aculeata* (Sterculiaceae) attract a variety of chalcid wasps, in addition to *Ectatomma* ants, thereby serving as an "insectary plant", affecting the insect community beyond serving as a host for its own herbivores.¹⁵² Censuses of visitors to *Byttneria* nectaries reveal ants and parasitic Hymenoptera to be about equally frequent at the nectaries; ants spend more time at nectaries than in patrolling the plants; and seven species of parasitoid Hymenoptera, including some collected from nectaries, were reared from leaf-feeding herbivores. Hespeneide¹⁵³ suggests that these plants may benefit more from parasitoids visiting its nectaries than ants. A variety of parasitic wasps in the families Braconidae and Chalcidae were observed feeding at extrafloral nectary analogs, insect-induced wounds, on stems of *Baccharis sarothroides* in Arizona.²⁵⁴

At sites where ants are not present in great numbers, the nectaries can serve as attractants to parasitoids. Legume trees in the genus *Inga* have extrafloral nectaries and ant protection in Costa Rican lowlands; the same species of trees, occurring at upland sites where ants are scarce, have nectaries visited by parasitoids, and a significantly greater proportion of caterpillars from upland trees are parasitized than in the lowlands.²⁰²

In a study of vetches in England,²⁰⁸ the evidence of parasitoid abundance from baiting did not demonstrate clear differences between the subsites where overall ant abundance was high. Data on parasitoids at baits may not provide an accurate estimate of parasitoid activity, because visits by flying insects are often shorter than those of ants. It is likely that once ants are at a bait, parasitoids will not visit that bait or will be chased away if they try. More solid evidence of the presence of parasitoids comes from their actual capture at nectaries and of parasitization of herbivore larvae. In the same study, there was evidence that ants kept parasitoids away and caused the reduced levels of parasitization of herbivore larvae in the pods at sites where ants were abundant.

IV. INTERACTIONS BETWEEN NECTARY VISITORS AND EFFECTS ON PLANTS

A. ANT-TENDED INSECTS — INSECT ANALOGS OF EXTRAFLORAL NECTARIES

A variety of insects that feed on plants exude secretions and are tended by ants. Many Homoptera excrete honeydew as they feed on phloem sap,^{58,59,351} including aphids,¹⁹⁴ psyllids, scale insects,¹⁸ and treehoppers.^{130,355} Lepidopteran larvae of the families Lycaenidae¹⁰ and Riodinidae⁹³ have specialized nectar glands with associated eversible tentacles. A hypothesis for the evolution of extrafloral nectaries²² proposes that nectaries can divert the ants from tending Homoptera, thereby reducing the recruitment of ant-tended Homoptera and damage to plants from these herbivores, and selecting for extrafloral nectar production by the plant. They reason that nectar collection does not require as much energy from ants as Homoptera husbandry does; therefore, if extrafloral nectar provides an equivalent resource with less work, the Homoptera may be abandoned. However, a great many species with extrafloral nectaries also have Homoptera tended by ants (e.g., *Populus* and *Vicia*). A survey of Homoptera and host plants, divided into hosts with and without extrafloral nectaries, might reveal interesting patterns. If species with nectaries have markedly fewer ant-tended Homoptera, the Berra and Venable²² theory would have some support. It may be, however, that species with extrafloral nectaries have more than their share of Homoptera, as might be predicted if the Homoptera are exploiting "enemy free space".¹⁰

The presence of ants stimulates the production of honeydew from tended insects.¹⁵⁴ Ant attendance increased honeydew excretion by *Aphis craccivora* more than fivefold and altered the posture of the aphid larvae as well.³³⁴ Exclusion of *Formica rufa* from *Periphyllus testudinaceus* aphids on branches of host trees in Britain resulted in a marked drop in the numbers of aphids.³¹⁸

In some cases, ants tending herbivores that are insect analogs of extrafloral nectaries can provide protection for host plants from other herbivores and increase plant fitness over conspecifics without tended herbivores. In order for the outcome of this interaction to be positive with respect to plant fitness, the ant-tended herbivore should not be the primary herbivore of the plant, and the ants should be effective against nonhomopteran herbivores. *Crematogaster africana* tending Homoptera on *Tapinanthus*, a mistletoe that grows on cocoa in Ghana, protect the mistletoe from other herbivores and allow greater shoot growth on plants with Homoptera and ants.³⁰³ Stout³³⁰ discovered Homoptera living in association with *Myrmelachista* ants inside hollowed-out stems of lauraceous understory trees in Costa Rica, and after observing the swift removal of insect eggs placed on young stems and leaves by the ants, hypothesized that the benefits to the plant in protection from herbivory by the ants outweigh the losses incurred by mealy-bug feeding. *Formica* ants tending *Publilia* treehoppers protect stems of goldenrod, *Solidago altissima*, from defoliation by chrysomelid beetles (*Trirhabda* spp.), resulting in greater seed production from plants with ants.²⁴³ Fritz¹²⁷ found no apparent harm or benefit to black locust in having *Vanduzee* *arquata* treehoppers and attendant *Formica subsericea* ants, because additional predators were important in the ant-herbivore interaction: while ants reduced adult density and oviposition of a leaf-mining beetle, *Odontota dorsalis*, they also excluded an important hemipteran predator of these beetles, *Nabicala subcoleoprata*, indirectly providing protection for the beetle larvae from this predator. Resident ants in myrmecophytic *Macaranga* in Southeast Asia tend scale insects inside the stems, and aid their host plants by removing young herbivores. In addition, they cleared them of other pioneer plant species by biting off foreign plant parts that come in contact with host trees.¹¹⁶

More typically, ants tending herbivores that secrete nectar decrease the fitness of the host plant. On Aldabra Atoll, the introduced coccid, *Icerya seychellarum*, utilizes a wide variety of plant taxa¹⁵⁵ and is tended by small numbers of various ant species during the day, and by large numbers of *Camponotus maculatus* during the night; ants reduce the numbers of a dipterid scale predator, *Chilocorus nigritus*, providing protection for the *Icerya* scale;¹⁵⁴ larger trees had heavier scale infestations and decreased shoot vigor.²⁵⁵⁻²⁵⁷ The interaction between ants and membracid treehoppers *Sextius virescens* has a negative effect on growth and seed set of Australian *Acacia decurrens*,⁵⁷ a host plant with extrafloral nectaries. Ants tending mealybugs on *Schomburgkia tibicinis* increase peduncle damage and inflorescence death, and reduce flowering and fruit set of the orchid.²⁹⁹

In a complex interaction, ants tending *Hilda patruelis* (Homoptera: Tettigometridae) on fig-producing branches of *Ficus sur* in south Africa reduce seed predation and parasitism of pollinating wasps by repelling nonpollinating wasps from the figs.⁶⁹ The net effect of the homopteran and its associated ants is beneficial for fig trees, as parasitism of the pollinator is significantly reduced wherever ant densities are high.

B. ANTS VS. PARASITIDS AND OTHER PREDATORS

Negative interactions between ants and parasitoids or predators of herbivores have been demonstrated in various nectar reward situations. In systems with extrafloral nectaries, and even more in extrafloral nectary analog situations, ants have been shown to protect certain herbivores (specialized either for ant resistance or for ant associations) from their enemies.

Herbivores that feed internally on plants with nectaries bear some resemblance to herbivores that have honeydew glands themselves, or form structures that exude honeydew, and may benefit in a similar way from the presence of ants at the secretions, since the aggressive behavior of ants toward other plant visitors will serve to drive away parasitoids. Cynipid gall wasps in Californian oaks are protected from their parasitoids by Argentine ants feeding on honeydew produced by the galls.³⁴⁸ Caterpillars eating leaves of lowland *Inga* trees (which are protected by ants visiting their foliar nectaries against many herbivores) were parasitized much less frequently than their higher elevation counterparts on *Inga* without ants.²⁰² Concealed feeders on *Vicia sativa* were parasitized less frequently in areas of high ant activity.²⁰⁸

Lycaenid caterpillars have glands on their bodies that exude honeydew, and tending ants that take this exudate protect the larvae from braconid wasp parasitoids.²⁸⁴ The larvae of the lycaenid butterfly, *Jalmenus evagoras*, are sometimes heavily parasitized by a braconid wasp, despite the presence of swarms of small attending *Iridomyrmex* ants.⁶⁸ Field experiments²⁸² demonstrated, however, that without the attendant ants, parasitism and predation of the immature stages are so intense that populations would not survive. Females use ants as an ovipositional cue,²⁸³ and the resulting local distribution of the butterfly is strongly influenced by the distribution of ants on their host plants.³²²

Many Homoptera derive benefits from their association with ants.³⁵¹ Nymphs of *Vanduzeeia arquata*, a treehopper that feeds on the sap of black locust in Maryland, are protected from their predators by aggressive *Formica subsericia*.¹²⁶ The saltbush scale, *Pulvinaria maskelli*, is tended by *Iridomyrmex*, which protect the scale from predators and climatic extremes, and enhance the damage suffered by the Australian host plant, *Atriplex vesicaria*.⁵³ Both aphid and membracid herbivores of New York ironweed (*Vernonia noveboracensis*) are protected by ants from their coccinellid and chrysopid larvae predators, but the aphids benefit more from association with *Tapinoma* ants, and membracids benefit more from association with *Myrmica* species.⁵⁴ In Arizona, *Formica*

altipetens tend the membracid *Publilia modesta*, and during some seasons they protect the nymphs from a predatory salticid spider.⁷⁸ Ants aggressively protect green scale from their coccinellid predators in coffee plantations.¹⁴⁵ More aggressive ant species provide better protection for soft scales and mealybugs against predators and parasitoids.⁶¹ The continuous day-and-night tending of Homoptera in the tropics may be especially important in protection from nocturnally feeding spider predators.⁶⁰

Of obvious importance to the interaction between ants and the other predators and parasites of herbivores is whether the herbivores are surface feeders or are concealed in various ways.⁷² For plants with extrafloral nectaries, ants are potentially effective at removing all external herbivores, except for those that are specialized to avoid ant defense or to benefit from it themselves (the various honeydew producers discussed above). Insects without the specializations to produce honeydew may also gain protection from ants tending extrafloral nectaries by living inside the plant tissues (in developing fruits, tied leaves, boring in stems, or occupying galls). The architectural complexity of plants is correlated with the diversity of herbivore species that utilize the plants;²¹⁶ at the next two trophic levels, parasitoid species richness is determined largely by host-plant architecture and herbivore feeding niche.¹⁴⁷ It would be of great interest to contrast herbivores from host plants with and without extrafloral nectaries to see if the richness of herbivores and parasitoids is influenced by the presence or absence of nectaries. I predict that plant species with extrafloral nectaries will have greater numbers of concealed or internal feeders, and may have lower parasitoid species richness as a consequence.

V. CONCLUSIONS

The myriad relationships between insects and plants mediated by extrafloral nectaries range from simple opportunism to mutual benefit and on to complex multiple interactions (both positive and negative). It is time now for biologists specializing in various groups of plants and arthropods involved in such interactions to test some hypotheses and to make generalizations where applicable.

The discoveries that herbivory can affect both the volume and composition of extrafloral nectar indicates a potential avenue of investigation for inducible defenses in plants with extrafloral nectaries. Does increased nectar volume result in greater visitation by insects? Does this result in more biotic protection against herbivores? Are increases in certain amino acids influencing visitation by various guilds of insects? Does this increase plant protection?

Extrafloral nectaries involved in pollination should be under selective pressures, as are floral nectaries, but some considerations differ. Do extrafloral nectaries respond to visitors by secreting more nectar? Or, like some floral nectaries, do they only produce a finite amount of nectar, not changing if visited?

We need to examine the distribution of honeydew-producing Homoptera on plants with and without extrafloral nectaries. Do plants with extrafloral nectaries have fewer Homoptera than congeners without? Is it possible that extrafloral nectaries were selected as ways of eliminating ant-tended Homoptera from plants?²² Or do Homoptera exploit plants with extrafloral nectaries as enemy-free space, like ant-tended Lepidoptera do?¹⁰

It would be of great interest to look at food webs based on extrafloral nectar. Nectar drinking is a special type of herbivory, yet the role of nectar in amplifying insect abundance in agricultural systems has been noted many times. Which of these insects are directly supported by nectar, or by insects that drink the nectar?

Whether or not a plant species has extrafloral nectaries may influence the structure of the herbivore community that feeds upon it. Do plant species with extrafloral nectaries have fewer herbivores than congeners without nectaries? Or perhaps a greater proportion of herbivores of certain guilds (e.g., concealed feeders)? And what about diversity of higher trophic levels (e.g., parasitoids) on congeners with and without nectaries?

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