PRUNING OF HOST PLANT NEIGHBORS BY ANTS: AN EXPERIMENTAL APPROACH[1]

DIANE W. DAVIDSON
Department of Biology, University of Utah, Salt Lake City, Utah 84112 USA

JOHN T. LONGINO
Department of Biological Sciences, University of California, Santa Barbara, California 93106 USA

AND

ROY R. SNELLING
Entomology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007 USA

Abstract. Some ants of myrmecophytic plants either obligately or facultatively prune vegetation surrounding their host trees. Pruning behavior occurs at higher frequency in ants with sting defenses than in those with chemical defenses, which may generally convey an advantage in aggressive encounters between ants. Experiments in tropical moist forest of Peru tested the hypothesis that pruning may reduce the threat of invasions by potentially dangerous alien ants.

When unseverable contacts were made between *Triplaris americana* 1–3 m in height and neighboring plants, *Crematogaster* ants invaded more frequently and in greater numbers than on control plants and inhibited activities of behaviorally subordinate resident *Pseudomyrmex dendroicus.* Invaders occasionally carried away brood and usurped hollow stem nests of resident ants. *Pseudomyrmex* cut petioles of leaves on plants contacting their hosts as well as leaves of their own host plants, when these leaves formed bridges for major invasions. Basal clearings maintained by *Pseudomyrmex* around their hosts appear to reduce the likelihood that *Crematogaster* workers will occur in the vicinity of the tree trunk.

On *Cordia nodosa* inhabited by *Allomerus demararae,* numbers of invading ants did not differ on experimental and control trees, perhaps because larger ants cannot invade through dense trichomes. *Allomerus* workers attacked encroaching vines only when these vines bore large numbers of *Crematogaster.*

Key words: allelopathy; Allomerus demararae; *ant–plant interactions; ants;* Cordia nodosa; Crematogaster; *mutualism; Peru; plant–animal interaction;* Pseudomyrmex; Triplaris americana.

INTRODUCTION

Janzen (1966, 1967*a, b,* 1969, 1972) has pointed out that plant-associated ants can act as allelopathic agents by pruning vines and other potentially competing vegetation from the vicinities of their host plants. When *Pseudomyrmex* colonies are removed from obligate ant acacias, plant growth rates and, presumably, fitness decline in response to increased rates of herbivory and shading by overgrowing vines (Janzen 1967*a*). By inference, ants should also benefit in the long term from the increased health and vigor of their host plants. Where fire frequency has increased due to habitat alteration by humans, ants as well as plants may benefit directly by clearing vegetation from a basal circle around the host plant. Such clearings reduce the destructiveness of fires to both acacias and their associated ant colonies (Janzen 1967*b*).

When understood in this framework, the origin of

such pruning behavior in ants is not easily explained (Beattie 1985). Attacks by ants on insect herbivores of host plants (potential prey) and on vertebrate herbivores (potential predators) can be interpreted as extensions of normal foraging behavior and colony defense, respectively. However, attacks on encroaching vines are more difficult to reconcile with the standard behavioral repertories of most ants. The origin of pruning behavior would appear to require a more direct and immediate advantage to ants than the advantages postulated above.

The distribution of pruning behavior over various ant taxa suggests an hypothesis for the origin of this behavior. Pruning is more common among ants with sting defenses than among those using chemical sprays in colony defense (Table 1, $P = .031$ in a two-tailed Fisher Exact Test). It is expressed most strongly in ants of the subfamily Pseudomyrmecinae (neotropical *Pseudomyrmex* and paleotropical *Tetraponera*), which rely heavily on sting defenses for colony protection (Blum and Hermann 1978). Sting defenses may be gen-

TABLE 1. Pruning behavior of plant-associated ants as a function of the defensive mechanisms of these ants.*

Ants	Plants	Pruning?†	Source
Ants with strong or weak stings‡			
Ponerinae			
Pachychondyla luteola	*Cecropia* sp.	Y[F]	D. W. Davidson et al., *personal observation*
Pseudomyrmecinae			
Pseudomyrmex spp.	*Acacia* spp.	Y[OB]	Janzen 1966, 1967a, 1967b
	Triplaris americana	Y[OB]	This study
Tetraponera spp.§	*Barteria fistulosa*	Y[OB]	Bequaert 1922, Janzen 1972
Myrmicinae			
Pheidole bicornis	*Piper* spp.	Y[F]	Risch et al. 1977
Pheidole minutula	*Maieta guianensis*	N	D. W. Davisdon et al., *personal observation*
	Clidemia heterophylla	N	
Allomerus spp.	*Cordia nodosa*	Y[F]	This study
	Duroia sp.	Y	A. Herre, *personal communication*
Chemically defended ants lacking functional stings‡			
Myrmicinae			
Crematogaster borneensis	*Macaranga triloba*	Y	D. W. Davidson, *personal observation*
Crematogaster spp.	*Acacia drepanolobium*	N	Bequaert 1922, Hocking 1970
Crematogaster cf. *victima*	*Tococa* cf. *Maieta guianensis*	N	D. W. Davidson, *personal observation*
Crematogaster parabiotica	Ant-garden epiphytes and host plants	N	D. W. Davidson, *personal observation*
Cataulacus mckeyi	*Leonardoxa africana*	N	McKey 1984
Dolichoderinae			
Azteca cf. *alfari*	*Cecropia* spp.	Y[O]	Janzen 1969
Azteca sp.	*Pleurothyrium* sp.	N	D. W. Davidson, *personal observation*
Azteca spp.	*Cordia nodosa*	N	D. W. Davidson, *personal observation*
	Tococa sp.	N	D. W. Davidson, *personal observation*
Formicinae			
Petalomyrmex phylax	*Leonardoxa americana*	N	McKey 1984
Camponotus femoratus	Host trees of ant-garden epiphytes	N	D. W. Davidson, *personal observation*

* Independent evolution of pruning behavior cannot be assumed for all pairs of congeners. Conservatively, we have chosen not to treat as independent samples the following three sets of congeners: (1) *Pseudomyrmex* species living on plant genera *Acacia* and *Triplaris*; (2) *Allomerus* species occurring on *C. nodosa* and *Duroia* sp.; and (3) *Azteca* species inhabiting *C. nodosa* and *Tococa* sp. For all other congeneric pairs, members of the pair occur in different generic subgroups.

† Y = yes, ants known to prune vegetation; N = no, literature on well-studied ants does not report pruning in any form; F = pruning is facultative, and not all attachments are pruned; O = pruning is obligate, and all attachments that can be pruned are pruned; B = circular plot at base of tree is cleared of vegetation.

‡ See Blum and Hermann (1978) for defenses of ant genera. *Crematogaster* species have a spatulate sting modified to administer contact toxins.

§ Genus includes ants formerly classified as *Pachysima* and *Viticola*.

erally inferior to chemical defenses in aggressive confrontations among ants. Although stings are often effective against solitary enemies (even a single ant may deter a vertebrate), they tend to be less useful against other social insects, especially those whose sophisticated chemical arsenals permit one worker to repel many ants simultaneously (e.g., Hölldobler 1982). We hypothesize that pruning of vines and other vegetation encroaching on hosts conveys an immediate or short-term advantage by limiting access to the host by competing and predatory ants and reducing fitness losses to these natural enemies. Thus, pruning is expressed most strongly in ants that are generally inferior in confrontations with other ants.

As further support for this hypothesis, we note the tendency for host plants of pruning ants to supply vir-

tually complete diets to their resident colonies (reviewed in Buckley 1982, Schemske 1983, Beattie 1985). Whatever the origins of pruning behavior, the complete diet may be necessary because workers tend not to forage off their host plants. Inferior competitive ability is a potential cause of extreme host plant fidelity (Davidson et al., *in press*).

To test our hypothesis, we examined the effects of bridges between neighboring vegetation and host trees with pruning ants. We studied two myrmecophytes in tropical moist forests of southeastern Peru. Here, *Triplaris americana* L. (Polygonaceae) is occupied by *Pseudomyrmex dendroicus* (P. Ward, *personal communication*, based on collections from 10 trees), and *Cordia nodosa* (Lam) (Boraginaceae) is inhabited by several ant species but most prominently by *Allomerus de-*

mararae Wheeler (Myrmicinae) (Davidson et al., *in press*). A diverse and abundant ant fauna includes not only several genera of army ants, but many ant genera and species that occupy these myrmecophytes elsewhere in the Neotropics (Wheeler 1942, Carroll 1983) and are potential competitors of *P. dendroicus* and *A. demararae*. The effects of pruning by the first of these species are very obvious, as *T. americana* regularly grows in circular plots (1–2 m diameter) almost devoid of vegetation. In contrast, vines sometimes encircle trunks of *C. nodosa*, despite their apparently large and healthy colonies of *A. demararae*. Nonetheless, the obvious isolation of actively growing branches of *C. nodosa* from contact with neighboring vegetation led us to suspect that the ants might, at least facultatively, prune vegetation impinging on their hosts.

METHODS

Our investigations took place at the Estación Biológica de Cocha Cashu, in the Parque Nacional Manu, Madre de Dios, Peru (elevation ≈400 m, latitude 11°52′ S, longitude 71°22′ W). Included within the station trail system is a mosaic of habitat types representing different seral stages of succession after disturbance by the meanderings of the Rio Manu (see Terborgh 1983). Experiments were begun in mid-September (end of the dry season) of 1985 and monitored closely for 6 wk. Several additional observations were made in September of 1986.

Small trees of *Triplaris americana* and *Cordia nodosa* were identified and tagged as encountered over portions of the trail system passing through "high ground forest" habitat, as defined by Terborgh (1983) for this site. Only trees 1–3 m in height were used. Individuals were assigned at random as experimental or control plants. Sample sizes were 12 experimental and 12 control plants for *T. americana,* and 24 plants in each of the two categories for *C. nodosa.* To each experimental plant, we attached a wire 1.5 mm in diameter. The opposite end of this wire was fastened to sturdy trunks or branches of surrounding vegetation. By using the wires to pull trees toward neighboring vegetation (chosen for proximity and at random with respect to activities of other ants), we established a number of contact points between experimental trees and sites from which other ants might invade. In each case, contacts were made between host tree branches and the branches and/or trunks of other plants. More easily severed contacts existed as well, for example, between leaves and stems, or leaves and leaves of the plants involved. Control individuals of the two plant species were not manipulated in any way.

All plants were censused visually for alien ants twice during the 10 d preceding the establishment of experiments, and once every 7–10 d thereafter for a period of ≈6 wk. Individuals of *T. americana* were also censused for workers of *P. dendroicus.* Leaves of this plant are thin, and ants on upper leaf surfaces cast silhouettes easily seen by an observer stationed below. So as not to affect ant activity levels during the censuses, the observer took care not to touch the plants and to census from as great a distance as possible. In contrast, on *C. nodosa,* whose dense trichomes obscured our view of the ants, accurate censuses required careful examination of all branches and considerable disturbance of the plants. Consequently, we were unable to measure activity levels of resident *A. demararae* under natural conditions. For each individual tree, numbers of invaders in the two pretreatment censuses were summed. Similarly, data for five posttreatment censuses were summed for individual control or treatment plants in comparisons of the total numbers of invaders per tree.

In each case in which invading ants were observed on control or experimental trees, we monitored interactions between invading and resident ants to determine which of the pair was behaviorally dominant. Ants classed as behaviorally subordinate turned away from encounters with dominant species. When the two species joined in combat, species were scored as having equivalent dominance. In a small proportion of cases in which neither species either retreated or attacked, no data were scored. An effort was made to obtain 10 independent estimates of dominance by scoring a single interaction for each of 10 invading workers in encounters with 10 different resident ants. However, some plants had fewer than 10 invading ants during the course of our observations. On these plants, we scored ≤10 encounters of individual workers of each invading species with resident ants. Invaders in successive censuses of the same individual plants were considered to be the same species if they looked superficially alike in the field. The conclusions of our study are unlikely to have been affected by failure to take behavioral observations on sibling species.

In October and November of 1986, baiting censuses were undertaken to test the hypothesis that the foraging activities of ants that are natural enemies of *P. dendroicus* are lower within clearings at the bases of *Triplaris* trees than on the ground outside these clearings. A small cheese bait was placed on the surface of the forest litter 10 cm north of each of 12 trees, each 1–3 m in height, but not including trees manipulated experimentally during the previous year. Simultaneously, an identical bait was placed on the litter surface outside the clearing 1 m north of the north clearing boundary. The occurrences of known natural enemies of *P. dendroicus* were monitored at both baits for a period of 30 min.

RESULTS

Triplaris americana

Experimental vs. control plants.—The numbers of invading ants on control trees and experimental trees were not normally distributed for either individual or grouped censuses, so we used nonparametric statistics
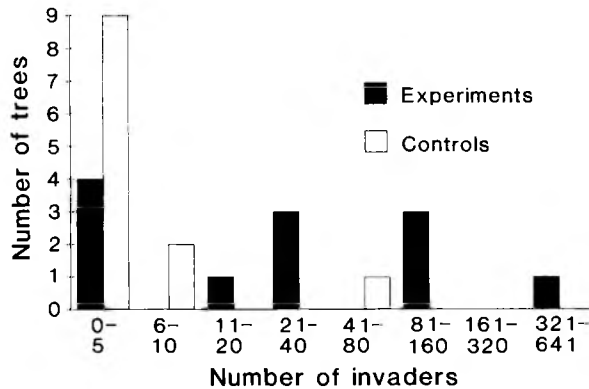
FIG. 1. Frequency distributions of experimental and control trees as a function of the number of invading ants (species other than *Pseudomyrmex dendroicus*) summed for five posttreatment censuses. The *x* axis is on a scale of $\log_2$, with the exception that the largest data point, 641, was included one category lower than it belonged. To have added another frequency class might have given the impression that the number of invaders was far greater than it actually was.

in all analyses. Comparisons of the numbers of invading ants on control and experimental trees of *T. americana* showed that the two groups did not differ significantly before imposition of experimental treatments (two-tailed Mann-Whitney $U_{[12, 12]} = 60.5$, $P \gg .05$). Control trees initially had slightly greater numbers of invading ants on average and, although three control trees had at least some invaders, this was true for only one experimental tree in pretreatment censuses. In posttreatment censuses, differences between control and experimental trees were highly significant (Fig. 1; one-tailed Mann-Whitney $U_{[12, 12]} = 118$, $P < .005$). On average, experimental trees were invaded by 14 times as many alien workers as were control trees. Significantly more experimental trees (8) than control trees (2) were invaded by some alien ants ($P = .018$ in a one-tailed Fisher Exact Test).

Ants used both attached wires and direct contacts between host plants and their neighbors to invade *Triplaris* trees. Most of the ants on control trees (63 of 85 in five censuses) were the result of a large invasion of one control tree during a single census by a colony of *Crematogaster brasiliensis*. The invasion occurred from a large, tough leaf (plant family Araceae) contacting the trunk of this tree ≈ 1 m above the ground. It is likely that workers of *P. dendroicus* could not sever the thick petiole of this leaf.

The most prominent genus of invading ants was *Crematogaster* (Table 2). At least 10 trees were invaded by a single species in this genus, *C. limata parabiotica*. Workers of *P. dendroicus* were behaviorally subordinate to this ant and to all but one species of invader for which behavioral dominance was scored (Table 2). In all cases where sample sizes of individual ants were adequate to compare a single worker's behavior to the

aggregate behaviors of 10 workers, the results were identical.

During invasions of both control and experimental trees, workers of *Crematogaster* and other ants moved unimpeded along branches and over the upper and lower leaf surfaces. *Pseudomyrmex* frequently retreated to their stem nests when *Crematogaster* workers were nearby, and remained there, often for extended periods, until these workers left. We observed no instance of interspecific combat but *Crematogaster brasiliensis* on one control tree, and *C. limata parabiotica* on two experimental trees, invaded hollow stems and returned with tiny white prey that proved under microscopic examination to be eggs.

During 6 wk of posttreatment monitoring, no experimental plant was taken over completely by invading species. However, experimental tree 5, which experienced a particularly heavy invasion by *C. limata parabiotica,* eventually had five of its seven growing tips taken over by the invaders. Persistent disturbance of the branch tips elicited no activity by *P. dendroicus* workers on these branches. Despite the contribution of this single tree, where activity of resident *Pseudomyrmex* declined drastically as *Crematogaster* increased (Fig. 2), experimental trees did not average significantly fewer workers than did control trees, either before or after treatments were established ($P \gg .05$ in both cases in Mann-Whitney *U* tests). In part, this lack of significance reflects the presence on invaded

TABLE 2. Invaders of *Triplasis americana* trees and outcomes of interspecific behavioral interactions.

Ant species	Total no. ants	Trees invaded*	Behavioral dominance†
Myrmicinae			
Crematogaster limata parabiotica	995	2C, 10E	I (83)
Crematogaster brasiliensis	214	1C, 1E	I (20)
Solenopsis sp. 3	5	1E	I (5, 5)
Formicinae			
Camponotus femoratus	8	3E	I (7, 3)
Camponotus sericeiventris	1	1E	I (3)
Dendromyrmex nidulans	9	1E	I (7, 3)
Dolichoderinae			
Dolichoderus imbecillus	2	1E	I (5, 3)
Ponerinae			
Unknown species	1	1E	R(2)

* C = control trees; E = experimental trees.

† I = invader behaviorally dominant; R = resident *Pseudomyrmex* behaviorally dominant. In parentheses are numbers of invading workers for which a single interaction was scored (roman type) and numbers of interactions scored for individual ants for which the results of multiple interactions were recorded (italic type). All behaviorally dominant invader species lacked stings or had very weak stings (e.g., *Solenopsis* [*Diplorhoptrum*]) and are representatives of chemically defended ant groups (Blum and Hermann 1978).

tree trunks of significant numbers of nonforaging work-ers alternately advancing toward and retreating from invading *Crematogaster*. For example, such behavior accounted for the high activity of *Pseudomyrmex* in Census 3 of Fig. 2.

In September of 1986, 1 yr after initiation of exper-iments, all or part of seven experimental trees but no part of any control tree was controlled by ants other than *P. dendroicus*. This difference is significant at $P = .002$ in a Fisher Exact Test. Two experimental trees and a total of five of eight branches on three other experimental trees were dominated by *C. limata para-biotica* to the exclusion of *Pseudomyrmex*. An addi-tional experimental tree contained an ant-garden nest shared by *C. limata parabiotica* and *Camponotus fe-moratus*, whose workers foraged over the entire plant. Although not active externally on their host plant, *Pseudomyrmex* workers were present in all seven branch tips of this plant. Finally a colony of *Azteca* ants with carton nests inhabited one experimental tree where no *Pseudomyrmex* activity could be elicited by disturbing branch tips.

Pruning of vegetation by ants. — When experimental trees were connected by artificial bridges to neighboring vegetation, workers of *P. dendroicus* did not appear to forage over the newly created avenues to this vegeta-tion. However, they did move onto live plants in con-tact with their host plants to sever the leaves of these plants at their petioles. Ants severed leaves on these plants regardless of whether the leaves were themselves bridges to the host plant, and regardless of the presence of enemy ants. The smallest of the pruned trees or treelets were dead by the following year. Severed leaves that fell onto the leaves of one host plant were not removed from the host plant's foliage, but remained there for weeks until swept away by wind and rain.

On three experimental plants, major invasions of *Crematogaster* occurred over host plant leaves that had been forced to contact stems or trunks of neighboring vegetation. In each of these cases, individuals of *P. dendroicus* cut the petioles of these host plant leaves on their lower surfaces. On one occasion, such a leaf was actually severed and fell from the plant. In each of the two remaining cases, ants ceased their efforts when the invasions subsided, and host plants retained their leaves. However, the damage was sufficient to cause the leaves eventually to droop from their nor-mally horizontal position and to discolor. In most other experimental *T. americana*, at least some host plant leaves contacted branches or trunks of neighboring vegetation. However, in no other case were major in-vasions occurring by these routes, and resident ants did not attempt to cut petioles of host plant leaves.

Finally, basal clearings pruned by *Pseudomyrmex* around their host plants appear to significantly reduce the activities of *Crematogaster* ants in the vicinities of these hosts. *Crematogaster* discovered only 2 of 12 baits within these clearings but 7 of 12 baits in sur-
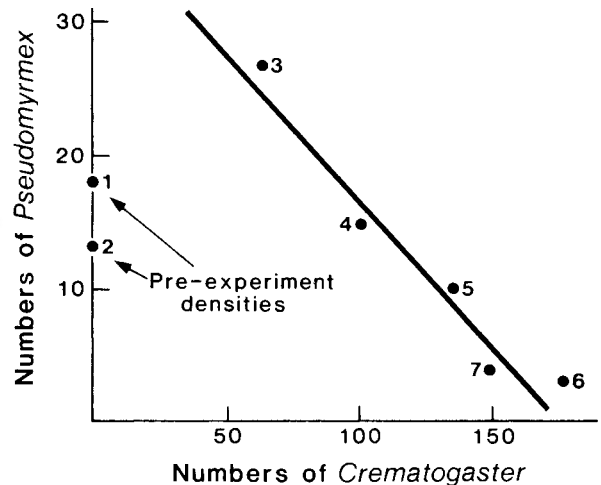

FIG. 2. Pretreatment (1 and 2) and posttreatment (3-7) population of *Pseudomyrmex dendroicus* foraging externally on experimental tree number 5, as a function of the number of invading *Crematogaster* visible externally on this tree dur-ing successive censuses. Inverse relationship between num-bers of *Crematogaster* and numbers of *P. dendroicus* is sig-nificant at $P < .01$ ($y = 38.80 - 0.22x$; $r = 0.97$).

rounding vegetation. This difference is significant at $P = .04$ in a one-tailed Fisher Exact Test.

Cordia nodosa

Numbers of invading ants did not differ significantly on control and experimental *Cordia nodosa* trees be-fore or after experimental manipulations ($U_{[24,24]} = 288$, $P = 1.000$, and $U_{[24,24]} = 60.5$, $P \gg .05$). No alien ants were observed on any plant during pretreatment cen-suses, and posttreatment censuses documented inva-sions of only one experimental tree (nine ants in one census) and one control tree (one ant in one census). Again, the invaders were species of *Crematogaster* (not collected for identification). In both cases, large worker forces of *Crematogaster* were foraging on vines as these vines made contact with trees of *C. nodosa*. On the invaded control tree, contact came as a result of natural growth of the vine, but on the experimental tree, con-tact between the tree and the vine was made artificially.

In each case, neither *Allomerus demararae* nor the invading *Crematogaster* retreated from combat, and species were scored as having equivalent behavioral dominance. However, their smaller body size enabled workers of *A. demararae* to move rapidly through the long, dense trichomes, or epidermal hairs, that cover the stems and leaves of *C. nodosa*, and to attack the larger *Crematogaster*, which were impeded by tri-chomes. Thus, *A. demararae* suffered fewer casualties in subsequent combat. Eventually *A. demararae* killed or drove away all invading *Crematogaster* and suc-ceeded in severing the delicate growing tips of the vines. Vine tips eventually turned black, perhaps indicative of necrosis caused by stings administered by *A. de-*

mararae workers. In contrast, vines without invading ants grew around the trunks of 5 of our 48 study trees and were not molested in any detectable way by the ants inhabiting these trees.

Observations in September of 1986 revealed that no experimental or control plant had been taken over in whole or in part from *A. demararae*.

DISCUSSION

Our results suggest that pruning of vegetation surrounding host trees of *Triplaris americana* limits potentially dangerous invasions by enemy ants (Fig. 1), most of which use chemical defenses and are behaviorally dominant (Table 2) to resident *Pseudomyrmex dendroicus*. In ants, success in defending nest sites and food resources is often a function of behavioral dominance (Wilson 1971, Hölldobler 1984). *Crematogaster* workers can enter the nests of behaviorally subordinate *Pseudomyrmex* to prey on brood. Invasions by these ants can disrupt the foraging activities of *Pseudomyrmex* workers (Fig. 2) that scour the leaves and stems of their host plants for plant-produced substances (D. W. Davidson, *personal observation*). Based on observations outside the context of these experimental studies, invading *Crematogaster* also kill *Pseudomyrmex* workers on occasion (D. W. Davidson, *personal observation*).

At least three kinds of observations suggest that pruning by ants of *T. americana* and *Cordia nodosa* is primarily a response to natural enemies rather than a means of stimulating productivity of the host plant and the colony over the longer term by the creation of light gaps. First, workers of *P. dendroicus* cut leaves of their own host plants when these leaves serve as bridges for major invasions by enemy ants. Second, a consequence of connections to surrounding vegetation is that resident *Pseudomyrmex* colonies are likely to lose control of all or part of their host plants' resources in the short term, so that longer term benefits may not be realized. Finally, pruning by *A. demararae* is facultative and tied to the presence of alien ants. Nevertheless, these kinds of evidence do not rule out the possibility that *Pseudomyrmex* and *Allomerus* colonies benefit over the longer term from increased light levels attributable to pruning by these ants. Our brief study did not address this question.

Our results also identify a possible selective advantage for the maintenance of basal clearings by *Pseudomyrmex* resident on *Triplaris*. By eliminating foraging substrate for leaf-foraging *Crematogaster*, *Pseudomyrmex* may reduce the likelihood that these preeminent invaders will invade via the host tree trunk. Interestingly, the only major invasion of a control plant occurred just slightly above ground level and from vegetation rather than the forest floor. As suggested earlier by Janzen (1967*a*), creation of basal clearings may also anticipate and preclude growth of potentially hazardous vines at some future occasion. In the moist

habitats where *T. americana* grows at Cocha Cashu, it seems unlikely that protection of plants or ants from fire (Janzen 1976*b*) is a significant advantage of these clearings.

Based on the measured abundance of *Crematogaster* in similar forests of southeastern Peru, it seems likely that these ants could exert major selection pressures on subordinate ant species. Analysis of the ant fauna collected by insecticidal fogging of trees at nearby Tambopata, Peru, identifies *Crematogaster* as the genus found most frequently in individual samples, and one of the two most common genera as measured by worker numbers (Wilson 1987). As in our study, the numerically dominant species of *Crematogaster* was *C. limata parabiotica,* a species that dominates individual trees of *T. americana* in some areas of Panama (Wheeler 1942).

In comparing the pruning behaviors of *A. demararae* with those of *P. dendroicus,* it is tempting to conclude that the facultative pruning exhibited by the former species is the "primitive" condition. While this scenario seems likely, there may be reasons other than history or limited evolutionary time why *A. demararae* fails to prune plants whose ant faunas do not pose an immediate threat to the resident colony. Only one experimental *Cordia* and one control plant were invaded by any other ants, though other ants appear to compete for this host plant at Cocha Cashu (Davidson et al., *in press*). The two invasions that did occur were successfully thwarted by resident ants. We attribute the paucity of invasions of these host plants to the presence of densely spaced trichomes on the leaves of *C. nodosa* (Davidson et al., *in press*). Hairs or trichomes are common among both New and Old World myrmecophytes (plant families Melastomaceae, Chrysobalanaceae, Polygonaceae, Rubiaceae, Sterculeaceae, etc.), and may generally function in excluding ants larger than a threshold size.

Individual trees of *C. nodosa* often appear to have few bridges to surrounding vegetation, despite the lack of direct evidence of frequent pruning of neighboring plants by ants. A factor contributing to this appearance may be the tendency for these trees to "discard" lower branches as they grow. In a brief survey of 10 *Cordia* matched with the closest understory trees of approximately equivalent size, *Cordia* were >8 times as likely to have an attached dead branch as were trees in the other sample (means of 1.7 vs. 0.2 dead branches per tree; two-tailed Mann-Whitney $U_{[10, 10]} = 89.5, P <$ .005). Unusually frequent dehiscence of branches also occurs in *Barteria fistulosa* (Bequaert 1922), a tree that hosts pruning ants in the pseudomyrmecine genus *Tetraponera.* We hypothesize that abcission of relatively unproductive branches in these two myrmecophytic trees (whether caused by the ants or the plants themselves) may reduce the probability that the plant contacts neighboring plants whose own ant faunas pose a threat to resident ants. Trichomes are not well main-

tained on older branches of *Cordia,* and pathways through these hairs might facilitate invasions by enemy ants. Other myrmecophytes such as *Triplaris* and *Cecropia* host stinging ants but do not have unusual numbers of dead branches on or beneath them. However, these trees have relatively unbranched growth forms that may make them more easily defensible by resident colonies of ants (Benson 1985).

Finally, our interpretation of pruning behavior leads to the unconventional hypothesis that pruning of neighboring plants by resident colonies of particular ants need not benefit the host plant. Thus, for example, pruning may enable resident ants to exclude more beneficial ant associates. Admittedly preliminary and indirect evidence suggests that this is not the case for *T. americana.* First, although we collected no systematic data on plant condition in relation to ant inhabitants, epxerimental plants and branches where *P. dendroicus* was displaced tended to have blackened stems bearing drooping, shredded leaves 1 yr after our experiments were initiated. In contrast, control and experimental plants or branches with *Pseudomyrmex* were green with leaves in generally good condition. Our observations are consistent with the experimental results of Oliveira et al. (1987), who report more effective and aggressive defense of *Triplaris surinamensis* by *Pseudomyrmex triplarinus* than by unnamed *Crematogaster* ants in western Brazil. Second, removal of all ants from young individuals of *T. americana* reveals the accumulation on leaf surfaces of a powdery yellow food substance for ants (D. W. Davidson, *personal observation*). Workers of *P. dendroicus* groom this material from tarsi and antennae onto their hairy sting sheaths and carry it to larval chambers. This food material is similar in form and distribution to the pollen grains and fungal spores upon which *Pseudomyrmex* ants typically feed (Wheeler and Bailey 1920), and it appears to alleviate the necessity for the ants to forage off their host plants and, thus, to maintain more numerous foraging routes to other vegetation. Despite the preliminary and inferential evidence suggesting mutualism between ants and plants, the precise nature of the relationships between *P. dendroicus* and *T. americana* and between *A. demararae* and *C. nodosa* remains to be elucidated.

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