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Patterns of Herbivory in a Tropical Deciduous Forest¹

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ABSTRACT

In the lowland deciduous and riparian evergreen forests of Guanacaste Province, Costa Rica, the insect seed predators are highly host-specific and display a variety of traits suggesting that the ways they use hosts are not randomly distributed. The vertebrate seed predators may feed on many species of seeds over the course of a year or within the animal population, but, at any one time or with any one individual, strong facultative host-specificity occurs. Furthermore, the vertebrates have a variety of species-specific behaviors that suggest specialization to overcome the defenses of particular seed species. Even the dispersal agents kill seeds as they pass through their guts, and the details of seed-defecation patterns should be important to the seed. Within this forest, leaf-eating caterpillars seem to be either specialized on one or a few species of plants, or spread over many. While an entire forest is never defoliated at one time, defoliations and severe herbivory occur with many plant species in various seasons or years. Herbivory by large herbivores is probably trivial when compared to that of the insects. Furthermore, the defenses that the large herbivores have to overcome may well have been selected for by both insects and extinct Pleistocene large herbivores. I suspect that many of the animal-plant interactions in this forest are not coevolved, and those that are coevolved will be difficult to distinguish from those that are not.

THERE ARE TWO QUITE DIFFERENT KINDS of 'patterns of herbivory.' First there is the way an individual herbivore bites a plant and the influence of this on other herbivores (Janzen 1973) and on the fitness, health, and growth patterns, et cetera of the bitten plant (e.g., Simberloff *et al.* 1978; Oppenheimer and Lang 1969; McKey 1978; Chester 1950; Janzen 1976a, b; Rockwood 1973). Much more research is needed on the allocation responses, economics of retention versus shedding of damaged parts, and strategic damage versus absolute damage. For example, the production of induced chemical defenses may raise the fitness of a plant not through the lowering of the absolute amount of herbivore damage done, but rather by causing the damage to be distributed in a manner that harms the plant less (Janzen 1979). However, this essay is not directed at this pattern of herbivory, but rather at the second one. This is the distribution of the species and quantities of herbivores across the mosaic of plant species, developmental stages, plant parts, habitats, defense types, and time. I focus on this pattern of herbivory in the deciduous forests, and their contained riparian vegetation and old pastures, in Santa Rosa National Park (SRNP), northwestern Guanacaste Province, Costa Rica (0-300 m elevation).

INSECT SEED PREDATORS

The lowlands of Guanacaste Province exclusive of the Nicoya Peninsula (about 3200 km²) have about

975 species of broad-leaved plants at latest count (Janzen and Liesner 1980). In an ongoing study of the insects that eat the seeds of these plants, at least 110 species of beetles (Bruchidae, Curculionidae, Cerambycidae) were reared from more than 3700 samples of fruits and seeds (Janzen 1980a). The seeds of at least 100 of the 975 species of plants were regularly found to have beetle larvae seed predators that develop in the seeds at the stage between nearly full-sized and mature (pre- and post-dispersal). Most of the species of beetles were specific to a particular plant species: 83 species (75%) preyed on one plant species, each of 14 preyed on only two, nine on three, and two on four. The bruchid *Stator pruininus* preyed on six species and *Stator limbatus* on eight species, and there was no overlap in their two prey lists (although all prey were legumes). Of the 100 prey species, 63 were in the Leguminosae, and the remainder were spread among 17 other plant families; however, only 17 percent of the broad-leaved plant species in the Guanacaste lowlands are in the Leguminosae.

I caution the reader to note that the extreme prey specificity described above is for one quite small portion of Central America. Based on specimens in the U.S. National Museum and other collections, it is clear that nearly all of these bruchids have ranges from northern South America or Panama well up into Mexico. Throughout such a long range it is very likely that a species of bruchid is locally adapted to different species of seeds in different areas (Janzen 1979). If the prey records are summed over a large geographic area, the beetle appears to be an extreme

¹This article is based upon a paper delivered at a symposium on the ecology of Costa Rica at Stillwater, Oklahoma, in 1979.

generalist. For example, *Stator limbatus* and *S. pruininus*, respectively, have 24 and 44 prey species known over their entire species ranges (Johnson and Kingsolver 1976). However, at any one site either of these beetles is acting as a predator on only a tiny subset of the species of seeds. It is this interaction that matters in the impact of these bruchids on plants, not how many prey species humans can tally over a gambit far greater than that of any population of the beetle.

Of the 100 prey species, 59 were fed on by a single species of beetle, 25 were fed on by two, 11 by three, four by four, and one (*Cassia leptocarpa*) by five (all species of bruchids). There were 163 cases of a beetle species attacking a prey species, and if these 163 attacks had been placed at random on 975 species of plants, 825 should have had no attacks, 138 have had one, 11.5 have had two, 0.6 have had three, 0.03 have had four, and 0.001 have had five. These values are highly significantly different from the observed categories ($X^2 = 117$, d.f. = 2, $p < 0.001$). There were too many unattacked species, too few that were preyed on by only one species, and too many that were preyed on by two to five species. This finding implies that either over evolutionary time most species of plants have been exceptionally difficult for the beetles to attack while a few have been exceptionally susceptible, or that when a new attack occurred it was more likely to happen to a species that had previously been attacked than to one that was previously unattacked. Two different processes could produce this latter pattern. A seed that is susceptible to predation by one species of beetle may simply lack effective defenses against beetle larvae in general; or second, an evolutionary response to beetle attack may be the evolution of intense seed-predator satiation with a large crop of poorly defended seeds (Janzen 1969). This would in turn increase susceptibility to other species of beetles (Janzen 1980a).

With some striking exceptions, the prey species of a beetle species that preyed on more than one plant species were closely related. On the other hand, in those cases where there were two or more congeners of a prey species in the Guanacaste lowlands, an average of 5.8 species of congeners were not preyed on by a species of beetle that preyed on at least one member of the genus. There could be two quite different causes for a seed predator to attack congeners when it attacks more than one species of seed. It could be that congeners are most likely to have similar seed defenses. Once the beetle has overcome one defense it is well prepared to deal with a similar one.

On the other hand, it may be that congeners with recognition cues similar to those of the normal prey are much more frequently probed with oviposition "mistakes," and therefore more likely to be tried by a mutant, than are prey that are no more attractive to the ovipositing beetle than is a piece of bark or a rock. For example, *Amblycerus spondiae* oviposited on a number of *Eugenia salamensis* seeds mixed in howler monkey feces rich in *Spondias mombin* nuts (the normal host of *A. spondiae*). The larvae developed normally and produced apparently healthy adult *A. spondiae* (Janzen 1980a). This event suggests that *E. salamensis* seeds are potential myrtaceous prey in this habitat, yet *A. spondiae* may never come to prey on them regularly because their odor cues are so different from those of anacardiaceous nuts that *A. spondiae* females will not recognize them as something on which to oviposit.

The patterns of prey distribution for these seed predator beetles in the study area are not all taxonomic. All eight species of *Caryedes* bruchids feed on the seeds of vines in two legume subfamilies (*Bauhinia glabra*, *Dioclea megacarpa*, *Centrosema plumieri*, *C. pubescens*, *Galactia striata*, *Calopogonium caeruleum*). *Acanthoscelides zebratus* preys exclusively on the seeds of *Mimosa pigra* in the portion of Guanacaste north of Santa Rosa National Park while *Acanthoscelides quadridentatus* does so to the south of SRNP. It is probably not coincidence that the three lowland tree species in lowland Guanacaste with distinctive intra-population synchronized supra-annual seed years (*Andira inermis*, *Hymenaea courbaril*, *Ateleia herbert-smithii*) have their seeds attacked by *Cleogonus*, *Rhinochenus*, and *Apion* weevils (Curculionidae), respectively, while Bruchidae generally attack those species with a moderate number of individuals in fruit every year. Seed weevils are generally more robust animals than bruchids and can often feed on foliage as adults, a facility which should help them in passing the two or more years between seed crops.

Viewing a fruit and its contained seeds as a habitat, the distribution of coleopterous seed predators within that habitat is certainly not a random selection of the total behaviors shown by the large array of beetle species that attack seeds. Almost every imaginable method of seed and fruit attack and subsequent location of larval development occurs, yet in Guanacaste at least 80 percent of the species usually attack in the following manner. The eggs are attached directly to the surface of the full-sized and nearly mature fruit, and the larvae hatch within one or two weeks. The larvae then mine through the fruit wall

into a seed, the coat of which is thick and firm but still soft at this time. One or a few larvae grow to full size feeding on the contents of that one seed. The last instar larva cuts an exit hole nearly through the seed coat and pupates in the seed. The adult emerges one to three weeks later. If the fruit has not dehisced by this time, the adult then cuts another exit hole through the fruit wall or uses one cut by a previous emergent. It is conspicuous that larval or pupal dormancy in the seed has not been encountered in any of my rearings. I suspect that an adult's chances of survival are much greater as a free-living individual than when encapsulated in a seed or fruit that may be eaten by fungi, vertebrates, or insects, or that will be either severely heated and desiccated (dry season-fruiting species) or water-soaked (wet season-fruiting species).

It is likewise conspicuous that beetle larvae do not mine into seeds and fruit until the seed is nearly full-sized, even though the adult beetles are present in the habitat throughout the many months of young fruit development, and therefore could have oviposited on the fruits at any point during fruit development. There may not be enough nutrients in a seed during its early developmental stages, but this supposition does not explain why the larvae do not mine through the fruit, eating young seeds as they go (as do a number of pyralid moth larvae).

However, there are several more likely causes for delayed oviposition. First, the younger a seed, the more likely that a plant will perceive the damage and cut off nutrient flow to a doomed offspring. Second, the larger the attacked seed, the larger are the unattacked seeds in the same fruit and the greater the return to the parent for each further resource unit invested in them. Thus, the more developed the attacked seed, the less likely is the plant to abort the entire fruit. Fruit abortion dumps the larva into a hostile environment with fewer defenses and nutrients than it would have were the fruit to remain attached to the plant. It is striking that in those cases where a beetle larva mines from seed to seed through the fruit (e.g., *Guazuma ulmifolia*, *Cassia emarginata*), the fruit is usually mature at the time of seed predation.

Finally, it is conspicuous that in almost all cases the beetle larvae feed exclusively on seed contents. When they also feed on fruit tissue, it is only as they are moving from seed to seed or moving from the outside of the fruit to the seed. Without doubt the seed contains the highest nutrient value per bite and to the beetle larvae with the ability to detoxify the seed's defenses, the seed is defenseless (though of

course the beetle larva bears the metabolic costs of this detoxification). However, this restriction is still puzzling since many species of moth larvae feed exclusively on immature fruit tissues.

Turning away from the study of coleopterous seed predators, there are two other large groups of insect seed predators spread over the habitats in SRNP: microlepidopteran moth larvae and sucking bugs. Both groups attack seeds at all stages and are not so conspicuously grouped into the "nearly-full-sized-seed-to-mature-seed" or "developing-flower-bud" stages as are beetle seed predators.

Pyraustine and phycitine pyralid larvae are very commonly encountered mining in fruits and seeds in SRNP. I have reared at least 18 species, but only one appears to have more than one host plant; the larvae of *Omiodes stigmatalis* (Pyraustinae) graze the florets on the insides of full-sized but immature figs on two very similar species of *Ficus* (*F. ovalis* and *F. cotinifolia*). While immature fruit content might seem to be a fairly monotonous food type, and therefore the immature fruits of many species should be available to a single moth species, there are physical, behavioral, and chemical traits of each fruit species that probably demand fairly complex responses by the moth larva for fruit- and seed-eating. For example, at the time the phycitine pyralid larvae that attack the pulp in the ripening fruits of *Hymenaea courbaril* are ready to exit as adults, the indehiscent fruit rind is extremely hard. To counter this condition, the larvae form a group of cocoons with the head ends all pointed at a spot on the fruit wall where one or more of the larvae has cut away the rind to form a paper-thin door. This thin area is punched out by the first moth to emerge. However, there may be some more polyphagous seed predator moth larvae in the habitat. An unidentified species of phycitine recently reared from the nearly mature seeds of *Ateleia herbert-smithii* (Leguminosae) looks extremely similar to the one that attacks the nearly mature seeds of *Bauhinia unguolata* (Leguminosae). Such euryphagy seems mandatory in the case of the microlepidopteran seed predator of *A. herbert-smithii* because the SRNP population of this tree produces fruit crops at only two- or three-year intervals (*B. unguolata* lives in the same habitat and fruits annually).

There is a moderately species-rich array of coreid, pentatomid, scutellarid, pyrrhocorid, and lygaeid nymph and adult bugs distributed over the SRNP bud, flower, and green fruit resource. Many of these, in contrast to the beetle and moth larvae seed predators, are quite polyphagous, though at a particular time of year a particular species is found primarily on

a particular species or plant part. Being generally much larger than the seed parts they feed on, these bugs kill many individual seeds and ovules during their lifetime. By probing the center of the developing ovule or seed and extracting just that part that is edible to them, they may well be removing the most nutrient-rich portions and avoiding the portions and stages that have well-developed chemical defenses. In other words, their polyphagy may not involve nearly as much versatility as would be required by a bruchid larva that could develop within the seeds of eight different families of plants. The nymphs and adults of one species of *Hypselonotus* (Coreidae) feed on seeds and ovules of at least this many families of plants at SRNP. On the other hand, certain kinds of seeds are very hard for a bug to penetrate due to great fruit hardness or great distance between the pericarp and the seeds; in these cases the bugs that prey on the seeds appear to be restricted to a particular species of plant. However, they may be found feeding on shoot tips, flower buds, and fallen fruits when the immature fruits and seeds are not available.

Once seeds have been dispersed, there is a taxonomically quite different but even more polyphagous set of seed predator bugs that attacks them. I have examined only those that kill the seeds of Malvales and Moraceae, but, in each case, it appears that the bugs (Pyrrhocoridae and Lygaeidae, respectively) are capable of feeding on any species of seed in the family if they can get to it. I certainly do not mean to imply, however, that all seeds in the Moraceae, for example, are of equal quality to a lygaeid. Here, then, it appears that the pattern of herbivory will be determined by where the seeds fall, how concentrated they are at certain sites, how conspicuous they are, weather conditions, etc. The *Dysdercus* bugs (Pyrrhocoridae) kill dispersed seeds of *Sterculia apetala*, *Bombacopsis quinata*, *Malvaviscus arboreus*, *Sida* spp., *Ceiba aesculifolia*, and many malvalian herbs. They are perhaps most analogous, among the insect seed predators, to a forest floor mouse with a malvalian habit.

VERTEBRATE SEED PREDATORS

Viewed over the annual cycle, a given species of SRNP vertebrate seed predator is much more widely spread across the seed species than is any insect seed predator. However, at any given time, a particular vertebrate seed-predator species or individual is likely to be facultatively very monophagous. When a flock of several hundred *Aratinga canicularis* parrots finds a stand of *Lonchocarpus minimiflorus* trees in full

immature fruit, for as long as two weeks the birds may do all of their morning feeding on immature seeds in that stand. The ground becomes densely covered with husked *L. nitidus* fruits, and it is clear that the birds' digestive systems are handling largely this food type for long periods. The much-larger *Amazona ochrocephala* parrots do the same to the larger seeds of *Enterolobium cyclocarpum*, and the much-smaller *Brotogeris jugularis* does the same to the much-smaller ripe seeds of *Ficus ovalis*. For example, an adult *B. jugularis* that had been feeding all morning in a heavily fruiting *Ficus ovalis* contained the remains of about 4815 fractured but previously intact seeds. To accumulate this many intact seeds, it would have had to pick about 510 figs (2.13 per minute for four hours) and discard about 80 percent of the viable seeds in the figs it picked (on average, these birds only bit about 20 percent out of each fig picked and each fig contained about 47 viable seeds). A *B. jugularis* flock of about 100 birds attacked this tree every morning, and they alone could have removed about 51,000 figs per day. I estimated that this tree contained about 780,000 figs, and the birds visited the tree for at least 12 consecutive days. This flock of birds probably killed about 20 percent of the tree's seed crop directly by cracking seeds. By dropping figs and fig fragments to the ground below they indirectly killed many more. The viable seeds in the figs on the ground are no longer eligible for dispersal by bats, and the majority are killed by lygaeid bugs. However, some would be eaten and dispersed by large mammals foraging below the fig tree.

Birds have extreme mobility and therefore may daily seek out and return to widely scattered monospecific peaks of seed abundance. Small forest-floor rodents, on the other hand, would seem to be model generalist seed predators on fallen seeds. However, while a given species of rodent may feed on many species of seeds in one season, it is certain that at a particular time and place a small number of species of seeds often form the bulk of the diet of an individual rodent, and many species of seeds cannot be eaten in quantity if at all.

In SRNP, *Liomys salvini* (Heteromyidae) and *Sigmodon hispidus* (Cricetidae) are examples of this generalization. *L. salvini*, whose demography in Guanacaste deciduous forests and laboratory behavior have been studied (Fleming 1973, 1974, 1977a, b; Fleming and Brown 1975), is the primary mammalian forest-floor seed predator in most SRNP-forested habitats (Bonoff and Janzen 1980). In these habitats, *Enterolobium cyclocarpum* is a large and

widely scattered leguminous tree that drops a large crop of large fruits during the second half of the dry season. Each fruit is indehiscent and contains 5-20 large seeds. Where large mammals are common (horses, cows, and, presumably, mastodonts), the fruits are eaten almost immediately after falling, and some fraction of the seeds escape digestive seed predation (Janzen 1981a, b, c) and are defecated in dung. Where these large mammals are missing, the fruits lie on the ground and rot when the rains come. *L. salvini* is a thorough harvester of the *E. cyclocarpum* seeds from both the dung piles and the fallen fruits (fresh as well as rotten). The seeds are eaten directly and cached in the underground burrows of *L. salvini*. I suspect that the *L. salvini* in the immediate vicinity of *E. cyclocarpum* trees subsist largely on *E. cyclocarpum* seeds during the last third of the dry season and the first two months of the rainy season, while those in the forest far from *E. cyclocarpum* trees occasionally add them to their diet when a large mammal happens to defecate some in their vicinity. Under laboratory conditions *L. salvini* can live and gain weight for at least a month on a pure diet of newly germinated *E. cyclocarpum* seeds, can survive at least a month on dry hard *E. cyclocarpum* seeds, and cuts small notches in dry hard *E. cyclocarpum* seeds so as to germinate them for later consumption (W. Hallwachs, pers. comm.). It therefore has specializations in seed predation that elevate it well above the level of being an indiscriminate seed-collecting machine.

Immediately adjacent to the forest habitats occupied by *L. salvini*, and sometimes in them, *Sigmodon hispidus* is a very common rodent (Bonoff and Janzen 1980). If *S. hispidus*, a seedling- and foliage-eater, is placed on a pure diet of newly germinated *E. cyclocarpum* seeds, it dies within a few days; however, if the newly germinated *E. cyclocarpum* seeds are boiled, *S. hispidus* can maintain its body weight apparently indefinitely on such a pure diet (W. Hallwachs, pers. comm.). *E. cyclocarpum* seeds contain protease inhibitors (C. Ryan, pers. comm.), toxic proteins that are presumably denatured by boiling just as are the toxic lectins in black beans (Janzen *et al.* 1976). In short, *L. salvini* is not only specialized at harvesting and preparing *E. cyclocarpum* seeds, but it is also specialized at digesting them, at least in comparison with another small terrestrial rodent from SRNP. If this kind of inter-specific variability in treatment and use of seeds is common to all the different small mammals in a tropical forest, and I see much circumstantial evidence that it is, it is clear that these animals will generate an overall

pattern of seed predation approaching the complexity of that generated by the insects, even though based on many fewer species of seed predators.

The large mammals are usually assumed to be the most generalist of all the seed predators in a tropical deciduous forest. Their pattern of herbivory is considered the most opportunistic, most diffuse, and most unpredictable with respect to any given plant species or individual. However, I suspect that this is a very misleading view.

The interactions of horses, cows, and tapirs with seeds of *E. cyclocarpum* provide examples. When a tapir encounters a fallen guanacaste fruit crop, it is likely to ingest two to six of the 10- to 20-seeded fruits and spit about half the seeds out while chewing. Of the swallowed seeds, as many as 78 percent may be digested (Janzen 1981a). The animal is clearly a digestive seed predator. When a range horse has free access to Guanacaste fruits it eats three to 20 in a meal with 10 to 15 fruits being the usual number. It spits out about half the seeds (Janzen 1981b). It may digest 44 to 93 percent of the seeds swallowed, depending on the individual horse (Janzen 1981c). A range cow may consume 20 to 100 fruits per day if it has free access to them, and spits out less than 10 percent of the seeds. At least 80 percent of these seeds survive the journey through the cow, and this journey usually takes less than nine days. In both the horse and the tapir, the journey takes about 10 to 12 days on average and may last as long as 60 days (Janzen 1981c). Tapirs are relatively solitary forest animals that occur at low density and probably remove only a tiny fraction of the fruit crop of the *E. cyclocarpum* population. However, their habit of seeking out water in which to defecate provides the one microhabitat that should protect the *E. cyclocarpum* seeds in the dung from rodent seed predators. *Enterolobium cyclocarpum* tree seeds may remain dormant in water for many months. Horses occur in groups and would consume a large portion of the *E. cyclocarpum* fruit crop. Cows produce a small number of dung piles very rich in *E. cyclocarpum* seeds, and a slightly larger number each with a few seeds. They defecate in the same habitats as horses, and the seeds in their dung will have the same fate.

The pattern of consumption of *E. cyclocarpum* seeds by large mammals and its impact on the population of the tree is complex and depends at least on the proportion and number of fruits eaten by each kind of animal, the ratio of forest to grassland habitats included in the animals' seed shadows, the density of *Liomys* in the forested habitats, and the proximity of water in which tapirs can defecate. The pat-

tern will certainly not be random, but predicting its form for a given period requires substantial experimentation. Finally, the complexity described above is not unique to *E. cyclocarpum* trees. It appears that virtually all the animal-dispersed species of trees in SRNP will have similarly complex patterns of herbivory associated with their population recruitment.

INSECT LEAF EATERS

Insects eat much more of the living vegetation than just leaves and reproductive parts, but my experience in SRNP is limited to those that eat these portions of the plant. Leaf eaters (herbivores in the strict sense, leaf parasites, leaf predators, plant parasites) are spread over the vegetation and plant species in the SRNP forest in a pattern that is conspicuous for its heterogeneity with respect to practically every variable imaginable except for certain kinds of taxonomic bonds (e.g., Windsor 1978). I will illustrate this with a brief discussion of the host specificity of larvae of Sphingidae and Saturniidae in SRNP, with data drawn from the early stages of a long-term study.

In table 1 I have listed all the naturally occurring larval host records for 21 confidently determined species of Sphingidae (as of July 1979). In the forest from which these records were derived, I have collected 63 species of Sphingidae, and there are probably about four more species yet to be collected (W. A. Haber, pers. comm.). While a very preliminary conclusion, it seems that the sphinx moth larvae show no greater polyphagy than do the seed-predator beetles described earlier (Janzen 1980a). W. Haber, conducting a similar study near Cañas in the deciduous forest to the south of SRNP, and in the evergreen forest near Monteverde at a nearby but greater elevation (1300 to 1800 m), is finding a similar pattern and sphingid larval food-plant specificity. I can state with certainty that any particular species of sphingid larva is parasitizing substantially less than 2 percent of the 625 broad-leaf species of plants available within SRNP. Furthermore, the sphingids are not haphazardly sprinkled over the available taxa. As seems to be well known for sphingid larval hosts throughout the world (W. A. Haber, pers. comm.; Harris 1972), the SRNP sphingids are concentrated on only a few families, and the foliage of members of these families is generally rich in alkaloids, latex, essential oils, irritating acids, or other small toxic compounds (e.g., Rubiaceae, Solanaceae, Anacardiaceae, Euphorbiaceae, Apocynaceae, Moraceae, Vitaceae, Bignoniaceae). For example, Leguminosae constitutes

TABLE 1. Host plants known to date (August 1979) for Sphingidae larvae in Santa Rosa National Park.

Moth	Host	Number of rearings
<i>Aellopos titan</i>	<i>Randia echinocarpa</i> (Rubiaceae)	14
	<i>Randia karstenii</i> (Rubiaceae)	4
<i>Aellopos fadus</i>	<i>Genipa americana</i> (Rubiaceae)	5
<i>Agrius cingulatus</i>	Convolvulaceae	2
<i>Cautethia spuria</i>	Rubiaceae DHJ 11909	2
<i>Enyo ocyptete</i>	<i>Tetracera volubilis</i> (Dilleniaceae)	22
	<i>Sebastiana confusa</i> (Euphorbiaceae)	16
<i>Erinnyis ello</i>	<i>Stemmadenia obovata</i> (Apocynaceae)	1
<i>Erinnyis oenotrus</i>	<i>Cissus rhombifolia</i> (Vitaceae)	64
	<i>Cissus sicyoides</i> (Vitaceae)	3
<i>Eupyrrhoglossum sagra</i>	<i>Chomelia spinosa</i> (Rubiaceae)	9
<i>Isognathus rimosus</i>	<i>Plumeria rubra</i> , flowers only (Apocynaceae)	7
<i>Manduca lefeburei</i>	<i>Casearia sylvestris</i> (Flacourtiaceae)	16
	<i>Casearia corymbosa</i> (Flacourtiaceae)	4
	<i>Casearia arguta</i> (Flacourtiaceae)	1
<i>Manduca new species</i>	<i>Godmania aesculifolia</i> (Bignoniaceae)	23
<i>Manduca florestan</i>	<i>Macfadenyia unguis-cati</i> (Bignoniaceae)	2
<i>Nyceryx coffeae</i>	<i>Calycophyllum</i> <i>candidissimum</i> (Rubiaceae)	1
	<i>Brosimum alicastrum</i> (Moraceae)	7
<i>Pachylia ficus</i>	<i>Castilla elastica</i> (Moraceae)	3
	<i>Ficus insipida</i> (Moraceae)	2
	<i>Trophis racemosa</i> (Moraceae)	3
<i>Pachylioides resumens</i>	<i>Forsteronia spicata</i> (Apocynaceae)	14
<i>Perigonia lusca</i>	<i>Calycophyllum</i> <i>candidissimum</i> (Rubiaceae)	3
	<i>Guettarda macrosperma</i> (Rubiaceae)	3
<i>Protambulyx strigilis</i>	<i>Spondias mombin</i> (Anacardiaceae)	3
	<i>Astronium graveolens</i> (Anacardiaceae)	2
<i>Pseudosphinx tetrio</i>	<i>Plumeria rubra</i> , leaves (Apocynaceae)	27
<i>Xylophanes maculator</i>	<i>Psychotria nervosa</i> (Rubiaceae)	2
<i>Xylophanes turbata</i>	<i>Psychotria microdon</i> (Rubiaceae)	100's
	<i>Hamelia patens</i> (Rubiaceae)	21
<i>Xylophanes anubis</i>	<i>Psychotria nervosa</i> (Rubiaceae)	1

17 percent of the dicot flora of lowland Guanacaste (Janzen and Liesner 1980), yet W. A. Haber and I have not yet found a sphingid larva feeding on a legume.

There are 30 species of saturniid moths breeding in SRNP (1978-1980) and Saturniidae larvae are of the same approximate body weight as sphingid larvae (2 to 15 g in the last instar), but in the SRNP habitats they display a totally different pattern of herbivory. My rearing records are more incomplete than for sphingids but a given species usually has more than two species of host, and these are often in two or more plant families. The most dramatic example is *Hylesia lineata*. The 1979 rainy season was a year of high density for *H. lineata*, and I reared this moth from caterpillars found feeding naturally on the foliage of 47 species of plants in 19 plant families (table 2). Such polyphagy is traditionally thought to be the case for many species of Saturniidae. However, even *H. lineata* is not feeding on about 85 per-

Myrtaceae
Psidium guineense^b
 Ochnaceae
Ouratea lucens^a
 Rhamnaceae
Gouania polygama^a
 Rubiaceae
Calycophyllum candidissimum^d
Chomelia spinosa^a
Guettarida macrosperma^c
 Rutaceae
Xanthoxylum setulosum^b
 Sapindaceae
Allophylus occidentalis^c
Cupania guatemalensis^b
Paullinia cururu^b
Serjania schiedeana^b
Urvillea ulmacea^c
 Sterculiaceae
Byttneria aculeata^b
Byttneria catalpaefolia^b
Guazuma ulmifolia^d
 Tiliaceae
Luebea speciosa^c
Triumfetta lappula^a
 Verbenaceae
Lantana camara^a
 plus 6 questionables

TABLE 2. Larval host plants of *Hylesia lineata* in the uplands of Santa Rosa National Park, May-July 1979.

Bignoniaceae
Tabebuia rosea^a
 Bombacaceae
Bombacopsis quinata^b
 Boraginaceae
Cordia alliodora^b
 Chrysobalanaceae
Hirtella racemosa
 Elaeocarpaceae
Muntingia calabura^a
 Flacourtiaceae
Casearia arguta^b
Casearia sylvestris^c
Casearia corymbosa^d
Zuelania guidonia^c
 Lauraceae
Persea americana^b (introduced)
 Leguminosae
Acacia tenuifolia^c
Cassia biflora^b
Diphysa robinoides^c
Enterolobium cyclocarpum^c
Hymenaea courbaril^c
Inga vera^b
Lonchocarpus nitidus^c
Lonchocarpus costaricensis^b
Lysiloma auritum^b
Machaerium kegelii^b
Mimosa pigra^a
Myrospermum frutescens^b
Pithecellobium lanceolatum^a
 Labiatae
Hyptis pectinata^a
 Malvaceae
Malvaviscus arboreus^a
 Malpighiaceae
Banisteriopsis muricata^b
Byrsonima crassifolia^a
Stigmaphyllon ellipticum^a

^aOnly one host record, but caterpillar developed into normal moth.

^bCommon plant but caterpillar only rarely encountered feeding on it.

^cCaterpillar found on most individuals of this plant, but no severe defoliation.

^dCaterpillar found in large numbers on many individuals of this plant; severe defoliation in some cases.

cent of the species of broad-leaf plants in its habitat.

A comparison of other traits of *H. lineata* with the SRNP sphingids is instructive in understanding the two very different patterns of herbivory that they display. The very short-lived *H. lineata* lays all its eggs in one cluster, and does not feed as an adult; the larvae require 8-11 weeks to attain a final live weight of 2 to 3 g; and are individually protected by stout, strongly urticating, spines (cf. Pinango *et al.* 1977), silken diurnal resting nests among foliage, and the formation of dense groups during all instars but the last. The foliage they consume is rich in astringent phenolic compounds, for example, the foliage of *Zuelania guidonia*, a very popular food plant, is 40 to 45 percent dry weight phenolics (P. Waterman, pers. comm.). The taxonomic array of plants eaten by *H. lineata* overlaps with that consumed by the sphingids only in *Casearia* and three species of Rubiaceae.

In contrast, sphingids lay one or a few eggs on a host plant and live for several months as adults (W. A. Haber, pers. comm.); a 2-3 g last instar larva can develop in three weeks (and a 15 g last instar larva in four weeks). The larvae appear to be protected

only by various types of visual deception. As mentioned earlier, the foliage they consume appears to be rich in toxins of the kinds that could be detoxified or avoided by specialized enzymes.

I suspect that the saturniids exemplify the feeding pattern whereby a caterpillar can feed on many species of hosts but obtains few nutrients from the foliage of any single species, whereas the sphingid caterpillar can feed on only one or a few species of host but obtains much resource per bite or per day from the plant it feeds on. In SRNP, rearing records suggest that moth larvae in the Limacodidae and Arctiidae often conform to the saturniid pattern, while many Noctuidae, Geometridae, and leaf-rolling Pyralidae conform to the sphingid pattern. Both the saturniids and sphingids at Santa Rosa have the same sort of very wide geographic distribution as that mentioned earlier for the bruchids. Over these ranges, the sphingids accumulate many species of hosts, but, as with the bruchids, it is their local behavior as specialists that really matters in their pattern of herbivory.

Leaf-eating caterpillars at SRNP show distinctive patterns of herbivory quite aside from those associated with taxonomic categories. Again, using the sphingids and saturniids as examples, there is enormous inter-year variation in larval abundance and therefore in damage done to host plants. In the 1978 rainy season, for example, the following sphingid larvae of *Eumorphia satellitia*, *Manduca lefeburei*, *Xylophanes turbata*, and *Aellopos titan* were extremely common, and defoliation of their host plants was commonplace. In the 1979 rainy season, I found a combined total of only four larvae of these four species, and the larvae of a new species of *Manduca* was the only sphingid abundant enough regularly to defoliate their host saplings. In the 1977 and 1978 rainy seasons, I encountered no more than three *Hylesia lineata* larvae, while in the first half of the 1979 rainy season I estimated an average density of one last instar larva per four m² over many hundreds of hectares of late second-growth forest. When the adults from these larvae emerged in late July 1979, it was common for more than 100 adults to be attracted per night to a single 15 w fluorescent or black light. Such fluctuations were not restricted to moth larvae; in 1979 the larvae of a new species of *Dorynota* (a cassid chrysomelid) defoliated every large *Tabebuia impetiginosa* (*T. palmeri* of older literature) and severely damaged the foliage of virtually all saplings and seedlings of this tree in the understory. There was no sign of this beetle in 1978 or 1980. However, the ups of one set of herbivore

populations do not necessarily balance the downs of others. In the early rainy season of 1977 I carefully surveyed the caterpillar density in a small section of late secondary succession forest in SRNP (Janzen 1980c); visual examination of the site at the same time of year in 1979 recorded caterpillar numbers and species richness never exceeding 10 percent of that seen in 1977.

Reports of total defoliation of individual tropical forest trees are scattered through the tropical forestry literature (e.g., Anderson 1961). In table 3 I have listed a few of the more obvious examples of total defoliation observed in SRNP in the 1978 and 1979 rainy seasons. In addition, I have seen large individuals of the following species of trees better than 80 percent stripped of a leaf crop by leaf-cutter ants (*Atta cephalotes*): *Bombacopsis quinata*, *Cochlospermum vitifolium*, *Spondias mombin*, *Enterolobium cyclocarpum*, *Godmania aesculifolia*, *Cordia alliodora*, *Tabebuia rosea*, *Piper amalago*, *Hymenaea courbaril*, and *Casearia corymbosa*. In short, severe defoliation of individual plants is a fairly common event in the SRNP forests, but it is not very exactly synchronized within or between years. With respect to any given species of perennial plant, there is a distribution of damage each year. A few individuals show no damage, many show light to moderate damage, and a few are very heavily defoliated. In some years this frequency distribution is pushed toward the light end of the scale, and in others, toward the heavy end. It is also my impression that if a feeding-intensity distribution could be constructed for all the species in an area, the same would apply.

VERTEBRATE LEAF-EATERS

Only two vertebrate leaf-eaters have been studied in the kind of deciduous forest habitat found in SRNP. The food of howler monkeys (*Alouatta palliata*) has been studied in river-side forest running through deciduous forest (Glander 1975, Rockwood and Glander 1979), and I have offered a captive adult tapir (*Tapirus bairdii*) the foliage of 381 species of plants from a similar forest. If one views a leaf-cutter ant colony (*Atta cephalotes*) as a large, relatively sedentary, arboreal, subdivided cow, then a third large herbivore has been studied (Rockwood 1973, 1975, 1976; Rockwood and Glander 1979; Stevens and Hubble, pers. comm.). These three studies lead to a generalized statement on how the herbivory by individuals and each population of such large animals is spread over the vegetation. 1. The foliage of a very large number of species of plants is consumed. 2.

TABLE 3. Examples of better than 90 percent defoliation of plants by other than leaf-cutter ants in Santa Rosa National Park during the 1978 and 1979 growing seasons.

Tree species	Defoliator	Intensity
<i>Enterolobium cyclocarpum</i>	larvae of <i>Coenipeta bibitrix</i> (Noctuidae)	Throughout Guanacaste 1978, scattered individuals 1979
<i>Enterolobium cyclocarpum</i>	adults of one species of Meloidae	Scattered individuals 1979
<i>Zizyphus guatemalensis</i>	larvae of one species of Geometridae	All lowland trees 1978
<i>Tabebuia impetiginosa</i>	larvae and adults of <i>Dorynota</i> (Chrysomelidae)	All lowland trees 1979
<i>Bursera simaruba</i>	larvae of <i>Eunica monima</i> (Nymphalidae)	Scattered individuals 1978
<i>Bombacopsis quinata</i>	adults of one species of Meloidae	Scattered individuals 1978, 1979
<i>Pisonia macranthocarpa</i>	larvae of <i>Euscirrhopterus poeyi</i> (Noctuidae)	All lowland trees 1978, scattered upland trees 1978, 1979
<i>Psychotria microdon</i>	larvae of <i>Xylophanes turbata</i> (Sphingidae)	Large patches of lowland shrubs 1978
<i>Hamelia patens</i>	larvae of <i>Xylophanes turbata</i> (Sphingidae)	Scattered upland trees 1978
<i>Cassia emarginata</i>	larvae of <i>Anteos chlorinde</i> (Pieridae)	Scattered sapling individuals 1978, 1979
<i>Cassia emarginata</i>	adults of 1 species of Meloidae	Scattered individuals 1978
<i>Cassia emarginata</i>	larvae of 1 species of Noctuidae	Scattered individuals 1978, 1979
<i>Cordia alliodora</i>	larvae of <i>Cropia connecta</i> and <i>Cropia infusa</i> (Noctuidae)	Most upland trees 1978
<i>Diphysa robinoides</i>	larvae and adults of 1 species of <i>Isorbinus</i> (Curculionidae)	Scattered upland saplings and large trees 1978
<i>Sterculia apetala</i>	1 species of unidentified moth larvae	Lowland trees 1978, 1979
<i>Caesalpinia exostemma</i>	adults of <i>Phyllophaga</i> (Scarabaeidae)	Scattered lowland trees 1978
<i>Ceiba aesculifolia</i>	adults of unidentified beetles	Scattered upland trees 1979
<i>Solanum hazenii</i>	adults of <i>Taeniopoda varipennis</i> (Acrididae)	All lowland roadside large plants 1979
<i>Arrabidaea patellifera</i>	nymphs of <i>Taeniopoda varipennis</i> (Acrididae)	Most upland large vines 1979
<i>Godmania aesculifolia</i>	larvae of <i>Manduca</i> new species (Sphingidae)	Scattered upland large saplings 1979
<i>Casearia corymbosa</i>	larvae of <i>Hylesia lineata</i> (Saturniidae)	Scattered upland shrubs 1979
<i>Casearia corymbosa</i>	larvae of 1 species of Pyralidae	Most lowland shrubs 1978
<i>Cissus rhombifolia</i>	larvae of <i>Eumorphba satelliina</i> (Sphingidae)	Most upland vines 1978
<i>Randia echinocarpa</i>	larvae of <i>Aellopos titan</i> (Sphingidae)	Scattered upland shrubs 1978
<i>Melampodium divaricatum</i>	larvae of 1 species of Pyralidae	Scattered large upland patches 1979

Foliage is not consumed in proportion to its relative abundance. 3. More species of plants are ignored or rejected than are fed on. 4. Only specific parts of the vegetation of many acceptable species are eaten. 5. Flower, fruit, and seed parts of particular tree species are part of the diet. 6. There is very little overlap among the plant parts and species most frequently eaten by these three animals. 7. Within a species of host plant, some individual plants are fed on much more regularly than others for reasons unrelated to their location in the forest. 8. There is no single set of defensive plant traits that allows the prediction of neglect or avoidance of a given plant species. 9. The damage is much less omnipresent than that done by insects, but tends to be very intense at the level of the plant or plant part fed on at a particular time.

If we ignore the Pleistocene megafauna, the contemporary native fauna of large leaf-eaters in the SRNP forest appears to represent a relatively trivial portion of the overall herbivore threat and impact. The howler monkey troops are many kilometers apart, except in the dry season when they are concentrated in the evergreen riparian vegetation, but even then, troops are encountered at a frequency of only about one troop per 5 to 10 kilometers of creek or riverbed. The tapirs in SRNP have been free from

hunting for little more than five years, and their density in 1978-1980 appeared to be about 10 to 20 per km². Leaf-cutter ants may attain densities of as high as 250 colonies per km² in late stages of succession (60- to 100-year-old regeneration of old pastures), but in apparently undisturbed forests at SRNP a density of 1 to 10 colonies per km² is normal. Combined collared peccary and white-tail deer density probably averages about 2 to 10 per km². Variegated squirrels, white-face monkeys, spider monkeys, prehensile-tailed porcupines, ctenosaur and iguana lizards, and terrestrial rodents also eat foliage, but there is no evidence to suggest that they are a large, consistent and omnipresent leaf-eating threat.

Taken as a group, the big animals listed above are probably much less of a threat than are the leaf-eating insects. I suspect that the large herbivores are largely foraging on a food with defense properties generated by millions of years of persistent and intense herbivory by leaf-eating insects, but when a tapir encounters the urticating spines on mala mujer (*Cnidocolus urens*) it is undoubtedly dealing with a response to browsing mammals. However, it seems reasonable to assume that most of the obnoxious traits of the Euphorbiaceae were generated by insect herbivores. Only one large herbivore moves readily

through tree crowns, and therefore much of the vegetation is not even within reach of large herbivores.

However, it would be premature to view this as anything more than a working hypothesis. Replace a Pleistocene megafauna equal in density to that supported by the mix of deciduous forest and grassland in SRNP when cattle and horses ranged freely. The 108 km² of SRNP has supported an estimated 2000 head of cattle and horses, and even at this time (1975-1977) there were areas of many tens of km² with no sign of cattle or horses. Then give this vertebrate biomass the browsing versatility possessed by the contemporary African megafauna. The vertebrate biomass will undoubtedly rise as will the spatial and seasonal thoroughness of browsing coverage. Acacia-ants are thorough defenders of their plants against insects as well as vertebrates. I wonder how far into the past we would have to go to find these ants with a morphology and behavior similar to that of their African relatives; *Pachysima* on *Barteria* has a morphology and behavior admirably suited to deterring vertebrates and poorly designed to deter leaf-eating insects (Janzen 1972, McKey 1974).

In closing, I must draw attention to a major flaw in the data base that is used in herbivory analyses. We record damage intensity and location, observe the impact on plants, and identify what animals were responsible. We then make guesses about the annual and seasonal omnipresence of the damage intensity and type. From this analysis emerges an impression of the pattern of herbivory, and, we imagine, a picture of the pattern of herbivore impact on the vegetation and its components. This assessment is grossly inaccurate. Using the data we collect to construct a picture of the impact of herbivores on the vegetation is comparable to using the pattern and intensity of body counts in U.S.-fought wars to construct a picture of the impact of imagined or real hostility of nations to the United States. It is quite obvious that the perennial defense budget of the U.S. is far greater than the actual damage done in its wars. It is likewise clear that the largest impact of the herbivores on plants is in the strategic and actual costs paid to repel the herbivores that did not eat a leaf or seed. There are enormous discrepancies in accurately allocating defense and repair costs to the potential and actual damage.

COEVOLUTION

'Coevolution' has become very fashionable, a subject now spoken of by editors, granting agencies, and the popular press with the same self-contained discreteness as 'physiology,' 'ecology,' 'sociobiology,' etc.

I am afraid that those of us who use the word have not been very introspective about what it means (Janzen 1980b). I have not used the word 'coevolution' in this paper, though understanding the coevolution of herbivores with their food plants is an integral part of understanding the pattern of herbivory in the SRNP forest. There is a large problem. The historical origin of the word can be traced to Ehrlich and Raven's (1964) essay. To let other authors speak for me: "especially since Ehrlich and Raven's (1964) analysis of coevolution between butterflies and their larval host plants, the interactions between plants and herbivores have figured prominently in the literature on coevolution" (Futuyma and Gould 1979). The problem is that although Ehrlich and Raven's essay was on coevolution, the example was of the evolutionary radiation of a group of animals onto a large and diverse food source. 'Coevolution' of butterflies and their hosts is neither described nor analyzed, since there is not a single sentence about butterfly host plants evolutionarily responding to the presence of butterfly larvae, an event which is necessary, by definition, for coevolution to have taken place.

The reader should be careful to note that I did not say that butterflies and plants do not coevolve. Rather, I note that the seminal paper in coevolution contains the same class of flaw that is conspicuously present in a large number of 'coevolutionary' studies, including most of my own. In short, 'coevolutionary' studies characteristically identify actual or reasonably potential evolutionary change in one organism in response to the traits of another, and then assume the corresponding traits in the 'another' to be the evolutionary result of the first organism's selective pressures. Nature may work otherwise commonly enough that this can be a very misleading model, especially in understanding animal-plant interactions.

I suspect the following happens very frequently. For some ecological reason, the intensity of herbivory on a plant population increases. The plant lineage responds through the evolution of a defense trait. The herbivore responds by ecologically moving in part or totally onto other plants. The other herbivores that feed on the plant population then adjust evolutionarily and ecologically to this new defense system. Alternatively, the herbivore may come up with a mutant that avoids the defenses of the plant, and thereby the intensity of herbivory increases. The plant population ecologically adjusts to this, and its other herbivores evolutionarily and ecologically adjust to this change. No coevolution has occurred in either of the two cases. Then along comes an herbivore that for some evolutionary reason increases its intensity

of herbivory on a plant population. The plant population evolves a good defense, and the herbivore moves off into other less well-defended plants. The plant defense remains despite the removal of the original selective agent because it is a good defense against other herbivores. Here, coevolution has occurred, but the participants can no longer be identified.

Even pollination and seed-dispersal systems, interactions that appear to be beyond suspicion, require scrutiny. If African sunbirds were introduced to SRNP, an unsuspecting biologist would then quickly (and incorrectly) infer that they were coevolved with the various hummingbird-pollinated flowers with long, red, tubular corollas. When mastodons disappeared from SRNP, it seems very likely that tapirs and agoutis could have become major dispersers of seeds in fruits that seem well-adapted ('co-evolved') to mammal diets, yet which in fact were coevolved with mastodons. To generalize, when a new vegetarian animal arrives in a habitat, the first thing it will do is feed on those vegetative parts most poorly defended and ignore those best defended against it. Likewise, it will feed on those fruits that

have traits most likely to be intensely attractive to it. With no evolution having occurred, the biologist, describing the interactions at a later date, will likely conclude that ignored vegetative parts contain coevolved defenses against the herbivore, and that the traits of the fruits are part of coevolved mutualisms with the herbivore. Neither conclusion need be true. Viewed this way, a central question in the evolution of animal-plant interactions becomes 'Have we had a lot of coevolution of animals and plants *in situ*, within their habitats, or have we had a moderate amount of evolution and a lot of moving about of the participants to create the fine tuning in the interactions?' Coevolutionary biologists act by and large as if the former is the case, but I am beginning to suspect that the latter is also a major influence.

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