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Ecological Characterization of a Costa Rican Dry Forest Caterpillar Fauna¹

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ABSTRACT

The dry forests of Costa Rica's Santa Rosa National Park (11°N lat., 0–350 m elevation, 6 mo without rain, 900–2300 mm rain/yr) range from deciduous and 2 m tall to nearly evergreen and 30 m tall. This vegetation and a complex mosaic of secondary succession in old fields and pastures supports at least 3140 species of caterpillars. Butterfly caterpillars constitute only 11 percent of the species and less than 1 percent of the biomass. Although the moth caterpillars are very species-rich, each of the 725 species of vascular plants is attacked by less than 20 species of caterpillars. From the viewpoint of a species of plant, the caterpillar species richness in Santa Rosa is therefore substantially less than from the viewpoint of any of a number of extratropical tree species; they are fed on by many more species of caterpillars at a single location. Although Santa Rosa does have some species of caterpillars that feed on seeds, dung, detritus, bark, etc., more than 95 percent of the species eat green leaves. Of these, about 37 percent feed exposed on the leaf surface.

A Santa Rosa woody plant commonly loses 1–20 percent of its leaf area to defoliators during the first half of the rainy season and very little after that, but on rare occasions plants are totally defoliated. These defoliations are almost always committed by a single generation of 1 or 2 species of caterpillars feeding on their 1 or 2 sole host plants. Nearly all the species of Santa Rosa plants are not fed on by any given species of caterpillar either because the plants contain chemicals that render them unacceptable or because the caterpillar refuses to eat foliage that lacks a feeding stimulant. Simultaneously, it is the negative impact of inclement weather and carnivores on Santa Rosa caterpillar populations that prevents any given species of caterpillar from usually defoliating the few species of plants that it can eat.

The Santa Rosa carnivore fauna ranges from absolutely monophagous to highly polyphagous. Its caterpillar food supply fluctuates enormously with year, season, position in a season, and microsite. This favors generalized and flexible carnivores on the one hand, and strongly specialized carnivores on the other hand. Many caterpillars are not available to the carnivores because they are too cryptic to be found, personally well-defended by urticating spines or chemicals (and are aposematic), mimics of distasteful or dangerous caterpillars, or participating in predator-satiating synchronization of life-stages. Probably no carnivore recognizes more than about three kinds of prey or host: those that are perceived and rejected, those that are eaten or used directly when encountered, and those that require some special treatment. No two species of carnivores divide the many species of caterpillars equally among these three kinds of prey or hosts. Certainly no carnivore views the Santa Rosa caterpillar fauna as consisting of 3140 species.

Virtually all Santa Rosa caterpillar species share their host plants with less than 20 other caterpillar species (the average may be less than 5). This means that from the direct perspective of any one species of caterpillar, the Santa Rosa caterpillar fauna is quite small and potential competitive interactions are very limited in ecological time. Furthermore, actual direct competitive interactions are rare (if they occur at all) owing to the generally low density of caterpillars at any given point in space and time. However, there are many potential opportunities for indirect intra- and interspecific caterpillar interactions that are mediated through shared carnivores (such as parasitoid Hymenoptera and Diptera, diseases, vertebrates, spiders, etc.).

CATERPILLARS ARE THE LARVAE of Lepidoptera, and in most forests of the world they consume more living leaves than all other animals combined. The understanding of an herbivore fauna thus becomes in great part the understanding of the caterpillar fauna. My goal is to understand the herbivore fauna of Santa Rosa National Park, a semi-forested 10,800-ha preserve on the Pacific coastal plain (0–350 m elevation, 11°N lat.) of northwestern Guanacaste Province, Costa Rica (Fig. 1). This park contains some of the last (and tiny) remnants of original lowland dry forest (also called deciduous forest) on the Pacific side of Central America. Overall, the vegetation of Santa Rosa is a mosaic of abandoned pastures and fields, and of ≤400-yr-old secondary successional forest ranging from almost totally deciduous (Fig. 2) to nearly evergreen. The original

vegetation ranged from 2-m-tall totally deciduous forest on serpentine (peridotite) ridges overlooking the ocean, to 30-m-tall nearly evergreen forest on mesas, hills, and swales at 300 m elevation. This vegetation has been severely perturbed by ranching, burning, agriculture, logging, and hunting since the late 1500s; prior to that, at least some of it was subject to indigenous agriculture. The rainy season is approximately 6 mo long (May–December) and receives 900–2300 mm of rain; the dry season is essentially rain free. Additional characterization of the site can be found in Janzen (1981a, 1984a, b, 1985b, 1986a, b, d, 1987a–c) and Hartshorn (1983).

Here I offer an approximate ecological characterization of the caterpillar fauna of Santa Rosa. It is also the first attempt at an ecological characterization of the caterpillar fauna of any tropical habitat. The study began in 1977 and will continue. Upcoming findings will undoubtedly modify and enrich the patterns, but this approximate

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FIGURE 1. Location of Santa Rosa National Park in northwestern Costa Rica. The dotted line is the Interamerican Highway. The five most northern volcanos of the Cordillera de Guanacaste and Cordillera de Tilaran are indicated by their specific names.

image is intended to encourage others to explore entire caterpillar faunas in the habitats they know well.

There are only two biologically meaningful measures of the proximity of two trees. One is the influence of each

tree on the other, and the other is the response(s) to the two trees' proximity by some third organism. All other measures of proximity are anthropocentric conveniences, useful to humans but a restrictive way to portray biological reality. The same philosophy applies to the characterization of a caterpillar fauna. There is, at the least, the taxonomist's viewpoint, the host plant's viewpoint, the carnivore's viewpoint, and the caterpillar's viewpoint. Here I offer an approximation of these relatively different viewpoints, the amalgamation of which might be termed the ecologist's viewpoint.

METHODS

The facts and opinions expressed here are based on 10 yr of intense observation of the Santa Rosa caterpillars and adult Lepidoptera fauna in the wet and dry seasons, beginning in 1977. Moths have been intensively collected at 15-W blacklights and fluorescent white lights at fixed positions overlooking the forest canopy and through the forest understory. At four sites these lights were maintained almost continually for 3 yr and for 2–4 mo in each of the other years. Over 50,000 moths have been collected and prepared as museum specimens, but this is less than 1 percent of those examined. The rate of capture (at lights) of macromoths and large microlepidoptera that are new to the Santa Rosa collection has declined to an average of only about one per month, and I am certain that the figures for Santa Rosa in Table 1 are greater than 90

TABLE 1. Comparative species richness of the caterpillar faunas of three local continental sites with diverse successional histories and covering approximately 100 km².

Taxon	Santa Rosa National Park (11° N lat.)	Ithaca, New York (42° N lat.) ^a	Kevo Station, northern Finland ^b (70° N lat.)
Butterflies (incl. Hesperidae, Lycaenidae, Riodinidae)	345 ^c	105	21
Arctiidae <i>sensu lato</i> (incl. Ctenuchidae, Pericopidae)	90	41	1
Lymantriidae	5	7	0
Limacodidae	20	13	0
Cossidae	25	3	0
Sphingidae	84	34	2
Saturniidae	35	11	0
Mimallonidae	8	2	0
Apatelodidae	10	2	0
Lasiocampidae	5	5	2
Geometridae	400	206	46
Notodontidae	150	50	2
Noctuidae	800	487	22
Microlepidoptera (incl. Pyralidae)	1130	600	168
Miscellaneous	35	11	0
Total ^d	3142	1577	264

^a Based on the synoptic collection of Lepidoptera at Cornell University, and J. Franclemont, pers. comm.

^b Based on extensive Lepidoptera surveys (Koponen *et al.* 1982).

^c Butterflies other than Hesperidae, Lycaenidae, and Riodinidae are derived from DeVries (1983).

^d Totals should be discounted by about 3 percent to account for waifs or strays (nonbreeding species).

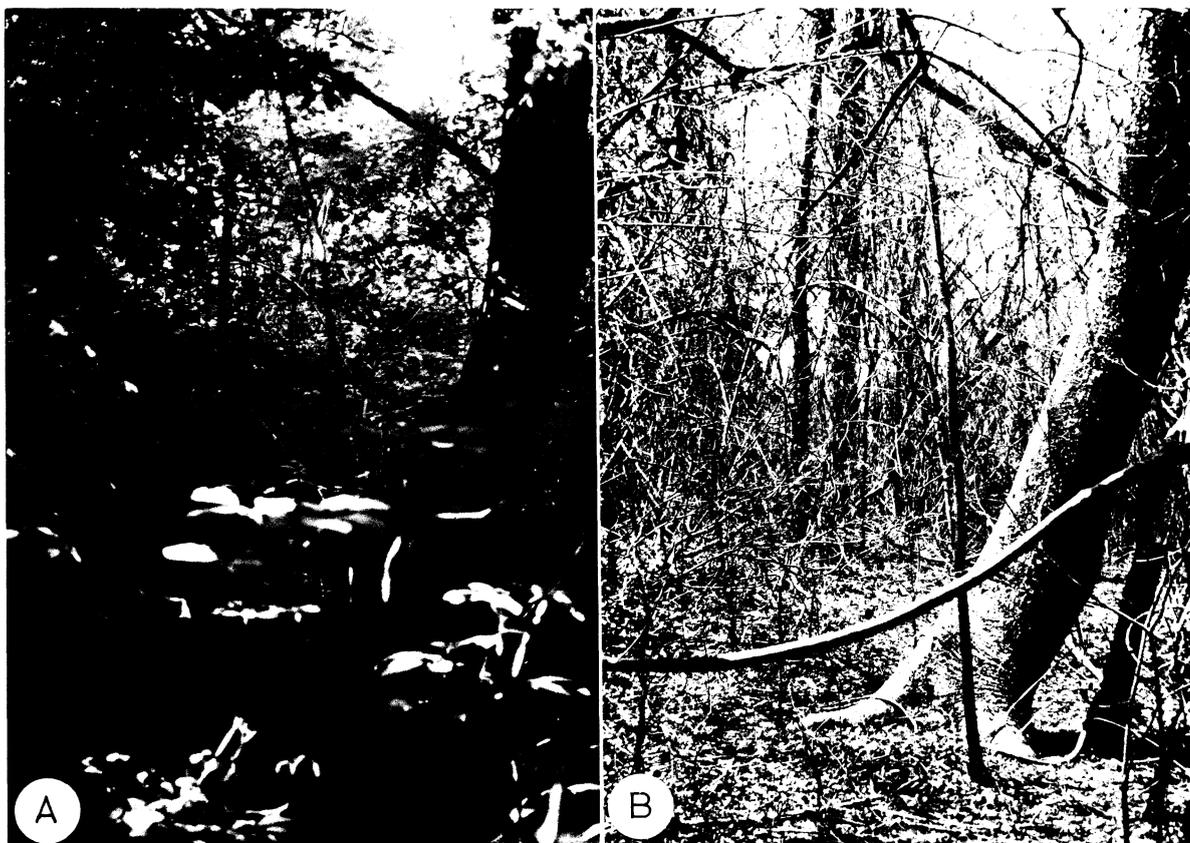


FIGURE 2. (A) 60- to 80-yr-old secondary successional dry forest in the first half of the rainy season (June). (B) Same view in the last third of the dry season (April).

percent of the real total for these groups. Some species of microlepidoptera have been as thoroughly collected (*e.g.*, Cossidae, Pyralidae, Oecophoridae, Tortricidae) as have been the macromoths.

Approximately 400 species of moths have been reared from more than 5000 wild-caught caterpillars, and only one of these species also has not been taken at the lights. Herbs, vines, shrubs, and trees in all habitats are searched for larvae. The complete fauna of saturniids and almost all sphingids has been collected and reared (Janzen 1984b, 1986d). Butterflies have been intensively collected by DeVries (1983), and further collecting and rearing of the hesperiids, lycaenids, and riodinids in the present project leads me to conclude that the butterflies have been relatively thoroughly collected. Leaf-mining and other microlepidoptera that do not come to lights have been estimated (Table 1) through conversations with taxonomists working in these groups, my observations of leaf and other kinds of mines, and rearing of microlepidoptera; P. A. Opler (*pers. comm.*) feels that this figure is as much as 30 percent too low, based on his rearing and observations

of leaf miners in the dry forests of the COMELCO area near Bagaces, about 70 km south of Santa Rosa.

I and numerous assistants have spent more than 5000 person-hours observing and rearing more than 10,000 accessions of wild-caught caterpillars (and their parasitoids) in Santa Rosa's dry forest. Free-living caterpillars have been obtained for rearing by virtually every conceivable kind of collecting, including cutting large branches out of tree crowns and inspecting their leaves, climbing trees with flashlights at night, and searching for the caterpillars that have dropped specific kinds of frass on sheets spread below trees (fogging with pesticides has not been used because the goal is to rear the caterpillars encountered). In the approximation of caterpillar ecology presented in this essay, I dwell only on those patterns that appear so emergent and/or repeatedly that they are unlikely to be significantly altered by further study.

Identifications of the plants and other organisms alluded to here are based either on my personal confidence in the names of organisms well known to those of us working in this forest (*e.g.*, Janzen & Liesner 1980, Janzen

1983a) or on specific determinations by specialists (see acknowledgments). All photographs were taken in Santa Rosa National Park.

THE TAXONOMIST'S VIEWPOINT

Since every species of moth and butterfly has a caterpillar (technically a "larva"), Santa Rosa is presently known to be occupied by about 3140 species of caterpillars (Table 1). However, this figure should probably be discounted by about 3 percent to account for nonbreeding strays (Janzen 1986c, 1986d). Such strays appear at about this frequency in large groups of Santa Rosa Lepidoptera whose residency status is well known (*e.g.*, butterflies, Saturniidae, Sphingidae, Noctuidae, Notodontidae, Pyralidae). As indicated earlier, the figure of 3140 is a composite of data from wild-caught adults and larvae, and estimations for some microlepidoptera families. The microlepidoptera may be underestimated by several hundred species (P. A. Opler, pers. comm.), but that underestimate will not significantly affect the conclusions presented here.

The Santa Rosa moth fauna is probably at its peak in species richness with respect to the near past and future. The progressive insularization of this piece of forest during the past 400 yr has probably not yet eliminated all the species that cannot persist indefinitely in the scattered fragments of the diverse habitats occurring in a dry forest area of 108 km² on diverse topography. Because Santa Rosa was an operating cattle ranch and a mosaic of rice fields, corn fields, selectively logged forest, and variously-aged old pasture succession when it became a national park in 1972, it now contains just about every imaginable kind of habitat and successional stage that can be derived from dry forest. As this habitat diversity is gradually reduced through succession to a relatively continuous (and eventually pristine) dry forest cover, some species of Lepidoptera will undoubtedly disappear. This should result in a net loss of species, because the maturing forests can no longer acquire a full pristine forest Lepidoptera fauna from areas adjacent to Santa Rosa. The pristine dry forest areas outside of the park were destroyed long ago.

Based on information in the literature, lepidopterist's folklore, and the rearing program in Santa Rosa, it is clear that its Lepidoptera fauna contains a smattering of seed predators (mostly phycitine and chrysaugine pyralids) and fruit miners (mostly pyralids; *e.g.*, Janzen 1983c), stem borers, gall borers or makers, detritivores, dung eaters, and carnivores. It even has a tineid microlep whose adult females ride on the backs of *Liomys salvini* mice from nest to nest (Davis *et al.* 1985). However, at least 95 percent of the species of Santa Rosa Lepidoptera are consumers of green leaves. Only approximately 37 percent of all of the species of caterpillars feed while exposed on the leaf surface, while the remainder are leaf miners, leaf rollers, or some kind of case-bearer. The comparable figures

for Ithaca, New York, and Kevo, Finland, are 59 and 36 percent, respectively. All three of these percentages were determined by characterizing the groups, or subgroups of them, in Table 1 as living either inside or on leaf surfaces. In short, a substantial fraction of the species in a caterpillar fauna lives inside of a plant part and is thus not generally available to foliage gleaners that do not penetrate or rip open plant parts.

Adult butterflies (including Hesperidae) are a very visible part of the lepidopterous fauna of any tropical site. However, they constitute only a small fraction of the species of Lepidoptera. At Santa Rosa, Ithaca, and Kevo, they are 11, 7, and 8 percent, respectively, of the fauna (Table 1). Their ecological insignificance is emphasized by the fact that they constitute well less than 1 percent of the biomass of caterpillars or adults at Santa Rosa. However, wildland butterfly biology has received far more attention (*e.g.*, Owen 1971, Gilbert & Singer 1975, Vane-Wright & Ackery 1984) than has that of moths.

Perhaps the most glaring trait to the taxonomist is that the Santa Rosa Lepidoptera fauna is not local or "endemic." Among the 35 species of saturniids (30 breeding residents and 5 strays) and 84 species of sphingids (74 usually-to-occasionally breeding residents and 10 strays), only one species is restricted ("endemic") to the area (Janzen 1984b, 1986d). This is *Schausiella santarosenensis*, a medium-large ceratocampine saturniid (Lemaire 1982, 1987) that seems to occur only in eastern Santa Rosa and thence to the lower foothills of the volcanic range 10–15 km to the northeast of the park (Fig. 1). This oddly restricted geographic distribution of about 500 km² occurs despite the fact that the caterpillar is a monophagous feeder on the leaves of a tree (*Hymenaea courbaril*, Leguminosae) that ranges from Mexico to Brazil. The remaining 118 species of Santa Rosa saturniids and sphingids have geographic distributions that extend over 10–60 degrees of latitude and occupy very diverse habitats (Janzen 1986d). Among the 345 species of butterflies, no local species or even distinctive populations have been encountered. Among the 150 species of Notodontidae known from Santa Rosa (more species than in all of North America north of Mexico; J. Franclemont, pers. comm.), none appear endemic to Santa Rosa.

Another conspicuous taxonomic trait of the Santa Rosa macrolepidoptera is that less than 20 percent were undescribed at the time the study began. There were no new sphingids, one new saturniid, five new notodontids, and approximately 15 new pyraustine pyralids. The reason why the Santa Rosa moth fauna consists of described species is not because collections were made in this part of Costa Rica by early collectors. Rather, each of the species in Santa Rosa was collected elsewhere in its large range. In short, the caterpillar phenotypes that survive in Santa Rosa also survive elsewhere; biogeographically, Santa Rosa has been a very ordinary place (Janzen 1986d). However,

Santa Rosa is now a forest island floating in an ocean of pasture and cropland. This insularization will undoubtedly take its toll of widespread species.

How species-rich is the Santa Rosa caterpillar fauna in comparison with that of other small and well-surveyed mainland areas? Two are tabulated in Table 1. The overall increase in Lepidoptera species richness that is encountered in moving from higher to lower latitudes is not equally intense for all families of Lepidoptera, but there is an approximate doubling in moving from Ithaca, New York, to Santa Rosa.

Five years of intensive collecting of moths at about 20 rainforest sites in Costa Rica (a country-wide moth survey, D. H. Janzen & W. Hallwachs, pers. obs.) have left the impression that Santa Rosa is about as rich in species of moths as are nearby lowland rainforest sites. This equality among dissimilar habitats is due in part to certain families being somewhat more species-rich in Costa Rican rainforests than at Santa Rosa (*e.g.*, Saturniidae, Geometridae), whereas others are less so (*e.g.*, Pyralidae, Noctuidae, Ethmiidae).

THE PLANT'S VIEWPOINT

There are approximately 725 species of vascular plants in Santa Rosa (Janzen & Liesner 1980, pers. obs.). The 3140 species of caterpillars are distributed quite unequally among them (numerous species of plants have only one species of caterpillar recorded from them to date). However, no species of plant, even large and common trees, is threatened by more than about 20 species of caterpillars in ecological time. For example, after 6 yr of intensive rearing wild-caught caterpillars in Santa Rosa, the record lepidopteran herbivore load is the 17 species of caterpillars that eat the leaves of *Manilkara chicle*, a common and large evergreen tree of pristine and old secondary successional forest (3 saturniids, 1 sphingid, 2 lycaenids, 2 notodontids, 1 mimallonid, 1 limacodid, 1 arctiid, 1 pyralid, 2 noctuids, 2 geometrids, and no leaf miners). Another tree with an exceptionally large fauna (15 spp. of caterpillars) is *Calycophyllum candidissimum* (Rubiaceae). There is no hint that the herbaceous plants in the park are supporting more moth species lists that are on average any longer than those of the woody plants. At this date in the sampling, it is too early to calculate either a reasonable overall average or standard deviation, but judging by the rate of addition of new host records for particular plant species, I estimate that the average will be between 4 and 8 species of caterpillar per plant species.

A plant at Santa Rosa therefore differs greatly from plants of similar individual sizes in more northern latitudes, where a tree species is commonly fed on by many tens of species of caterpillars (*e.g.*, Niemela & Neuvonen 1983). A Santa Rosa tree will view a tropical forest as being quite species-poor in caterpillars, whereas an Ithaca or Kevo tree

will view the forest as being quite species-rich in caterpillars.

Even the average figures are a misleading indicator of what is experienced by a plant. The Ithaca, New York, area has about 1580 species of caterpillars (Table 1). Tömpkins County, New York, which roughly approximates the area surveyed for the Ithaca Lepidoptera census, contains about 1800 species of native vascular plants (R. Wesley, pers. comm.). Kevo, in northern Finland, has about 260 species of caterpillars (Table 1) and 248 species of native vascular plants (Makinen & Kallio 1979). On average each of the two extratropical sites has about one species of caterpillar per plant species, as compared with a little more than four per host species at Santa Rosa. However, the direction and intensity of this gradient in averages certainly does not reflect the species richness of the interactions between a tree and its caterpillars at each of the sites.

Another question to ask a plant is how much damage it sustains from caterpillars:

REDUCTION IN LEAF AREA.—On an annual basis, the herbivore loads in Santa Rosa remove 1–10 percent of the expanded leaves retained by the tree. Another ≤ 10 percent of the leaf areas is removed in the form of leaves eaten entirely or leaves that are sufficiently damaged that they are shed by the tree. Certain species of Santa Rosa trees [*e.g.*, *Simarouba glauca* (Simaroubaceae), *Tabebuia rosea* (Bignoniaceae), *Guarea glabra* and *Trichilia americana* (Meliaceae), *Allophylus occidentalis* (Sapindaceae), *Hemiangium excelsum* (Hippocrateaceae)] experience almost no leaf herbivory. At the other extreme are trees whose leaf crop is often severely damaged by the end of its life [*e.g.*, *C. candidissimum*, *Alibertia edulis*, and *Genipa americana* (Rubiaceae), *Manikara chicle* (Sapotaceae), *Casearia corymbosa* (Flacourtiaceae), *Quercus oleoides* (Fagaceae), *Licania arborea* (Chrysobalanaceae), *Spondias mombin* (Anacardiaceae), *Guazuma ulmifolia* (Ulmaceae), *Luehea speciosa* (Tiliaceae)].

The small annual amounts of leaf damage are extremely difficult to measure directly, and their pertinence to any direct measure of plant fitness can only be determined by species-specific and habitat-specific experiments (*e.g.*, Marquis 1984). How these losses compare with the cost of the standing defenses that keep the other 3120–3140 species of caterpillars (and other herbivores) from eating the foliage of a tree is unknowable at present, but standing defenses are undoubtedly much more expensive than the usual annual damage to that plant. Incidentally, the proportion and absolute amount of the leaf damage done by insects other than caterpillars varies widely from year to year, conspecific to conspecific, and species to species.

TOTAL DEFOLIATION.—At long multiyear intervals, one of the species of monophagous or nearly monophagous (feeding on 2–3 closely related plants) caterpillars defoliates a

Santa Rosa tree or severely damages the leaf crop (e.g., Fig. 3). More than 40 such events have occurred in the past 9 yr at Santa Rosa (e.g., Janzen 1981a, 1984a, 1985a). Such a defoliation event normally lasts for only one generation, and the caterpillars are on the plant(s) for 2–3 wk. Usually the caterpillars that do the defoliation produce enormous numbers of healthy pupae, almost all adults eclose within a few weeks, and they then disappear (in many cases, apparently migrating away from Santa Rosa, Janzen 1986d, 1987b). There is normally no hint of even the beginning of subsequent defoliating generation. Even those individual host plants that are still leafy after the defoliation event (normally because they were cleaned of caterpillars by carnivores such as ants, spiders, true bugs, and vertebrates; e.g., Janzen 1985a) are not heavily fed on further during that season. In the one case where a second defoliating generation was initiated by the relatively polyphagous saturniid caterpillars of *Hylesia lineata*, the second generation was conspicuously terminated before pupation by a virus disease (Janzen 1981a, 1984a, b).

Such defoliating events occur at such long intervals that to date only one repeat performance has been observed. *Randia subcordata* and *R. aculeata* (Rubiaceae) were defoliated by a single generation of *Aellopos titan* (Sphingidae) caterpillars in the early rainy season of 1978 and 1983 (Janzen 1985a; one host was incorrectly identified as *Randia karstenii*). However, other repeats have occurred in which the caterpillars were extremely common, but not abundant enough to have caused conspicuous defoliation of their hosts.

Defoliations of trees (e.g., *T. rosea*, *Tabebuia impetiginosa*) by the leaf-feeding larvae of chrysomelid beetles at Santa Rosa follow the same pattern as that described above for caterpillars. However, monophagous species of adult meloid beetles (blister beetles) aggregate on a very few individuals of their host plants [e.g., *Pisonia macranthocarpha* (Nyctaginaceae), *Diphyssa robinoides* (Leguminosae)] and may strip off an entire leaf crop in one night. This occurs on an annual basis at the beginning of the rainy season.

Leaf replacement rates vary strongly among species. Leaves may be replaced almost immediately following a defoliation event [e.g., *S. mombin* (Anacardiaceae) defoliated by euteliine noctuids in 1984], after several months (e.g., *Randia* spp. defoliated by *A. titan*), or nearly a year later at the time of population-wide leaf turnover by the host (e.g., *M. chicle* after defoliation by many caterpillars of *Othorene purpurascens* that were experimentally maintained at a high density).

Reasons for the lack of a second successive defoliating generation vary among plant and caterpillar species. In many cases, the adults migrate out of the park, apparently to wetter forest in other parts of Costa Rica (Janzen 1984b, 1987c) where they pass the remainder of the Santa Rosa wet season and the Santa Rosa dry season. In at least one

case (*Perigonia lusca*, Sphingidae, in Janzen 1984b), and I suspect in many others, they pass one or more generations in the wetter forest (where the habitat is probably less carnivore-rich than Santa Rosa becomes after its first generation of caterpillars at the beginning of the rainy season). In other cases there is no suggestion that the adults migrate out of Santa Rosa. Some of these species of caterpillars spend the remainder of the year as pupae, and others pass a subsequent inconspicuous generation in the second half of the rainy season (Janzen 1987b); a third group of species has populations that contain individuals doing both things.

Whatever the behavior of the moths or caterpillars, defoliation events are clearly not normally directly extinguished by carnivores that build up on successive conspecific generations of caterpillars (*Hylesia lineata* has been the only exception). Caterpillar outbreaks at Santa Rosa generally sustain less than 5 percent parasitization by parasitoids (e.g., Janzen 1985a). By definition the vertebrate carnivores must have been satiated by the defoliators (or a defoliation event would not have occurred). On the other hand, migration or pupal diapause during the rainy (and dry) season can be viewed as the termination of a defoliation event by carnivores in evolutionary rather than ecological time. Were a moth to begin evolving in ways that led to successive high-density generations, it is easy to imagine its demise at Santa Rosa through the combination of carnivores and depletion of the foliage of its particular host species.

Clearly, 10 yr of rearing records and observations at Santa Rosa are inadequate for discerning inter- or intra-specific multiyear patterns to defoliation events. For example, the decade beginning in 1977 has had only one year without any species suffering a major defoliation and one year of defoliation of many species. However, the absence of repeat defoliations strongly suggests that a tree species that is defoliated is likely to grow for many years without being defoliated again (though during that period it is used as a host plant by its herbivore load at low density). Also, the impact (if any) of the Santa Rosa caterpillar fauna on the structure of arrays of plant species is through the subsequent growth and reproductive behavior of a defoliated species of plant, rather than through the more indirect pathway of a species of caterpillar building up to outbreak densities on one species of plant and then moving on to damage other species of plants in the same or subsequent generations.

HOST-HERBIVORE SPECIFICITY.—The species-poor caterpillar fauna of each Santa Rosa tree species is usually not widely shared with other species of host plants. For example, only one (*Erinnyis ello*, Sphingidae) of the 17 species mentioned earlier as eating *M. chicle* leaves also eats the leaves of three or more other tree species (and even in this case it is restricted to a few latex-rich species; e.g., Dillon *et al.* 1983; Janzen 1984b, 1985a). The arctiid also eats *Mastichodendron capiri* (Sapotaceae). The other 15 species





FIGURE 4. Ventral frontal view of a living spiny pocket mouse (*Liomys salvini*) that was carrying a prepupa of *Cautethia spuria* (Sphingidae) in one of its pouches. The head of the prepupa has been bitten off, and the entire insect would have been eaten later in the burrow.

appear to be monophagous. The host records accumulated to date suggest that when the final counts are done, at least half of the Santa Rosa caterpillars will be found to have only one host plant species at Santa Rosa, and at least 80 percent of the remainder will have just a few chemically or taxonomically related species of hosts (e.g., see the host lists for Sphingidae in Janzen 1984a, 1985a). The highly polyphagous species with 20+ species of host plants in numerous plant families [e.g., *H. lineata* (Janzen 1984a); *Hypercompe* spp., Arctiidae] are clearly a miniscule proportion of the caterpillar fauna.

In sum, each of the Santa Rosa plants "sees" (in ecological time) its habitat as containing only a small number of species of caterpillars. Because at least half the species of Santa Rosa caterpillars are monophagous, and

the remainder oligophagous to only a few species, the intensity of caterpillar challenge to a given plant species is not directly related either to the number of species of caterpillars in the habitat or to the details of the traits of nearly all of the other species of plants in the habitat. In other words, *H. courbaril* does not in any direct way experience the presence of the herbivore load that feeds on *T. rosea*.

Three observations suggest that plant defensive chemistry has little or nothing to do directly with the daily challenge by a plant's herbivore fauna in Santa Rosa: the members of that fauna obviously can eat the foliage of that plant species, there is no suggestion that leaf chemistry changes seasonally (either in the rearing records or in analyses; e.g., Jansen & Waterman 1984), and during the

FIGURE 3. (A) Crown of large adult *Acosmium panamensis* (Leguminosae) defoliated by a single species of noctuid caterpillar (June 1984). (B) Crown of *Annona purpurea* (Annonaceae) defoliated by caterpillars of *Gonodonta pyrgo* (Noctuidae); an undamaged vine of *Cissus rhombifolia* (Vitaceae) forms a rough X in the center of the *Annona* crown (June 1983). (C) Crown of *Enterolobium cyclocarpum* (Leguminosae) defoliated by a species of megalopygid caterpillar (cf. Fig. 9b) (October 1982).

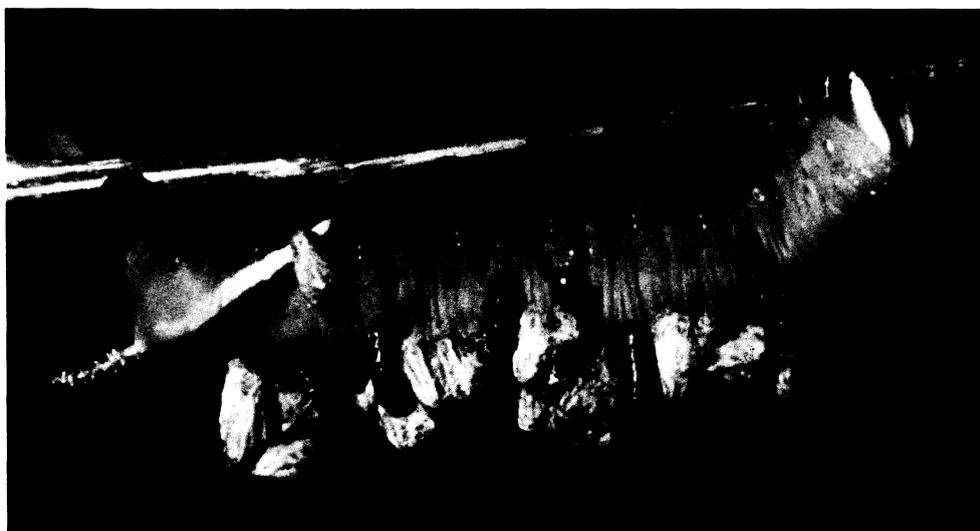


FIGURE 5. Last instar larva of *Manduca lefeburei* (Sphingidae) with a sib group of parasitic Hymenoptera (Braconidae) newly emerged from its body cavity and spinning cocoons.

second half of the rainy season the plants are in full foliage yet support almost no caterpillars. However, it is equally clear that plant defensive chemistry keeps the vast majority of caterpillar species (as well as fungi, microbes, and other insects) from eating the foliage of any particular plant species.

However, the intensity of caterpillar challenge to a Santa Rosa plant is directly related to climate and carnivore components of the habitat. And the carnivores, excepting the monophagous species, that feed on the caterpillars of any given plant species are at least in part sustained by the caterpillars that feed on some other species of plant.

THE CARNIVORE'S VIEWPOINT

Santa Rosa has an abundant and species-rich carnivore fauna. However, whether a Santa Rosa caterpillar leads a riskier life than does an extratropical caterpillar (*e.g.*, Janzen 1981b) has not been studied. Santa Rosa has many highly polyphagous vertebrate and invertebrate carnivores: coatis, *Nasua narica*; white-faced monkeys, *Cebus capucinus*; spider monkeys, *Ateles geoffroyi*; collared peccaries, *Dicotyles tajacu*; spiny pocket mice, *L. salvini* (Fig. 4); gray foxes, *Urocyon cinereoargenteus*; 9-banded armadillos, *Dasypus novemcinctus*; squirrel cuckoos, *Piaya cayana*; motmots, *Momotus momota*, *Eumomota superciliosa*; trogons, *Trogon* spp.; rufous-naped wrens, *Campylorhynchus*

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FIGURE 6. Adult *Enicospilus* parasitic wasp (Ichneumonidae) of a species that parasitizes only *Rothschildia lebeau* (Saturniidae) in Santa Rosa National Park.





FIGURE 7. Last instar geometrid moth caterpillar in resting position on its sole species of host plant, *Hymenaea courbaril* (Leguminosae). The caterpillar is the same shade of yellowish-green as are the stems and new leaves on which it feeds. The caterpillar is the terminal third of the "stem" and is holding tightly to the stem with its posterior prolegs at the point where the petiole of the second pair of leaflets leaves the stem. The caterpillar's shadow is marked sharply on the leaflet below it.

rufinucha; at least another 50 species of small birds that glean and otherwise harvest caterpillars; scorpions; spiders; ants; social wasps; carabid beetles, neuropterans; crickets; pentatomid bugs; reduviid bugs. There are also well over 300 species of caterpillar-eating and pupa-eating tachinid fly, ichneumonid wasp, and braconid wasp larvae (e.g., Fig. 5). The latter three groups of insect parasitoids range from absolutely monophagous [e.g., each of the three species of *Enicospilus* ichneumonid wasps (Fig. 6) that attack Saturniidae have only one known species of larval host at Santa Rosa] to attacking a cluster of related species (e.g., one species of *Belvosia* tachinid fly parasitizes *Rothschildia*, *Eacles*, *Citheronia*, and hemileucine saturniids; one species of *Belvosia* parasitizes the relatively small sphingids that pupate in the litter; and one species of *Belvosia* parasitizes the larger sphingids that pupate deep below the soil surface).

Most members of the Santa Rosa carnivore fauna can potentially encounter nearly all 3140 species of caterpillars on an ecological time scale. However, owing to selective foraging behavior by the carnivores, physiological and morphological incompatibility with prey and hosts, and

caterpillar escape traits, any given member of the carnivore array will make use of (is a threat to) only a very small fraction of the species of Santa Rosa caterpillars. To a trogon, for example, there are three basic "species" of caterpillars: those seen and rejected, those seen and eaten directly, and those seen and eaten but requiring special processing. There is a fourth "species" as well, the caterpillars never seen at all (e.g., Fig. 7); this is probably the most species-rich category for all carnivores. Within the first category of caterpillars are coral snake-patterned caterpillars (Fig. 8) that are presumably rejected because of genetically based fear or repulsion (e.g., Smith 1975, 1977). For example, the brightly ringed large caterpillars of *Rothschildia erycina* (Saturniidae) (e.g., cover photograph of Janzen 1983a) and *Arsenura armida* (Saturniidae) (Janzen 1982) are passed over by squirrel cuckoos, trogons, and other medium-sized caterpillar-hunting birds, but readily eaten by large lizards, *Ctenosaura similis* (pers. obs.). The latter example reflects the general phenomenon that a caterpillar that is rejected by one species of carnivore may be readily eaten by another; for example, white-faced monkeys reject urticating caterpillars (Fig. 9), but squirrel

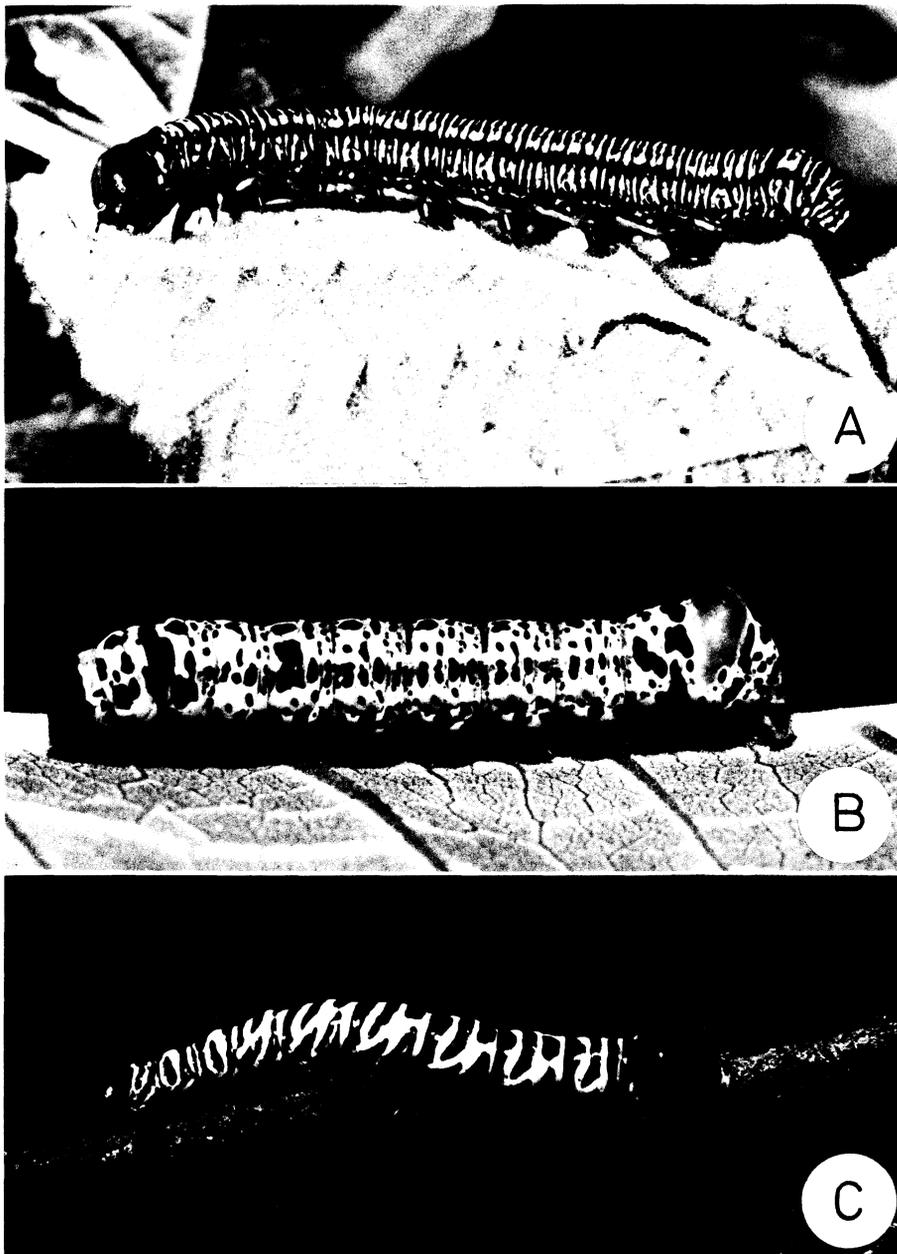


FIGURE 8. (A) Last instar caterpillar of *Diphthera festiva* (Noctuidae); the body is black and white, with a red head capsule and red posterior portion of the last abdominal segment, and an orange lower lateral area just above the abdominal legs (host plant: *Waltheria* spp., Sterculiaceae). (B) Last instar caterpillar of *Neophaenis respondens* (Noctuidae); it is black and yellowish-white, with a red head and red-orange dorsal bump at the posterior end (host plant: *Petreaea volubilis*, Verbenaceae). (C) Penultimate instar caterpillar of *Lirimiris guatemalensis* (Notodontidae); it is black and white, with a red head capsule and red dorsal bump at the posterior end (host plant: *Guazuma ulmifolia*, Sterculiaceae). All three of these species are Mullerian or Batesian mimics of the "coral-snake image" in a bird's mind, or classical models.

cuckoos eat them regularly (after first smashing the spines on a tree branch).

It is clear that the carnivores would not compare the caterpillar fauna of Santa Rosa with that of, for example,

a Wisconsin woodlot on the same basis as would a taxonomist. A foraging bird in Santa Rosa and Wisconsin might well conclude that the "species richness" of the two sites is the same (four "species" in each), although the

relative proportions of each are different. Likewise, the monophagous carnivores in both habitats would conclude that the diversity was identical in the two forests, since all the nonprey and nonhosts do not directly affect them.

The demographic and microgeographic properties of the Santa Rosa caterpillar fauna can affect carnivores in at least three major ways. Like the traits of individual larvae touched on above, these properties are not reflected in the lengths of faunal lists for the site.

CATERPILLAR DENSITY.—The overall density and biomass of caterpillars at Santa Rosa fluctuates enormously from year to year [for example, the caterpillar density in 1977 (Janzen 1980) was far higher than it has been in the 9 yr since]. However, overall measures of caterpillar biomass, species richness, caterpillar density, *etc.*, probably mean little biologically (*i.e.*, no carnivore is as polyphagous as are the generalized sampling techniques associated with these measures). The degree to which a particular carnivore individual or species is influenced by such fluctuations will depend largely on whether its particular prey or hosts are contributors to the fluctuation and whether other carnivores share its prey or hosts. This applied to polyphagous armadillos as well as to monophagous ichneumonid wasps.

SEASONAL CHANGE.—During the year, overall caterpillar biomass and density is close to zero during the 6-mo dry season (late December to early May), builds up rapidly during the first 2 mo of the rainy season (late May to mid-July), declines precipitously in late July and August, and then remains very low through the remaining half of the rainy season (*e.g.*, Janzen 1980, 1987b). This general pattern is most closely followed by the leaf-eating caterpillars. Heinrich and Collins (1983) have noted that foraging birds may cue on leaf damage as an aid in locating caterpillars in extratropical forests. In Santa Rosa, the accumulation of damage to the leaves is very rapid in the first month of the rainy season, and the caterpillars move a great deal from day to day. During later parts of the rainy season the damage persists, but no caterpillars accompany it. The consequence is that a damaged leaf is a very poor indicator of the presence of a caterpillar in Santa Rosa's forests.

The caterpillars of numerous species of seed- and fruit-mining microlepidoptera are most numerous during the dry season, and wood-boring caterpillars (Cossidae) appear to be present in moderate numbers throughout the year. However, these caterpillars are largely inaccessible to carnivores and so do not compensate the predators for the absence of foliage-eaters.

PREDATOR SATIATION.—Since different species of caterpillars appear in large numbers in different years, a carnivore's year-to-year perception of caterpillar density will depend on how polyphagous it is. There is, however, a distinctive

indirect interaction in this part of the ecosystem. A conspicuous outbreak of a species of highly edible caterpillar may satiate quite generalist carnivores (birds, monkeys). These carnivores will then search less for those species of caterpillars (or other insects) that are at low densities or on few species of plants in the habitat. For example, in years of high caterpillar density, there is conspicuously less damage by birds to the wings of large saturniid moths that rest (hide) in the foliage in the daytime than is the case in years of low caterpillar density.

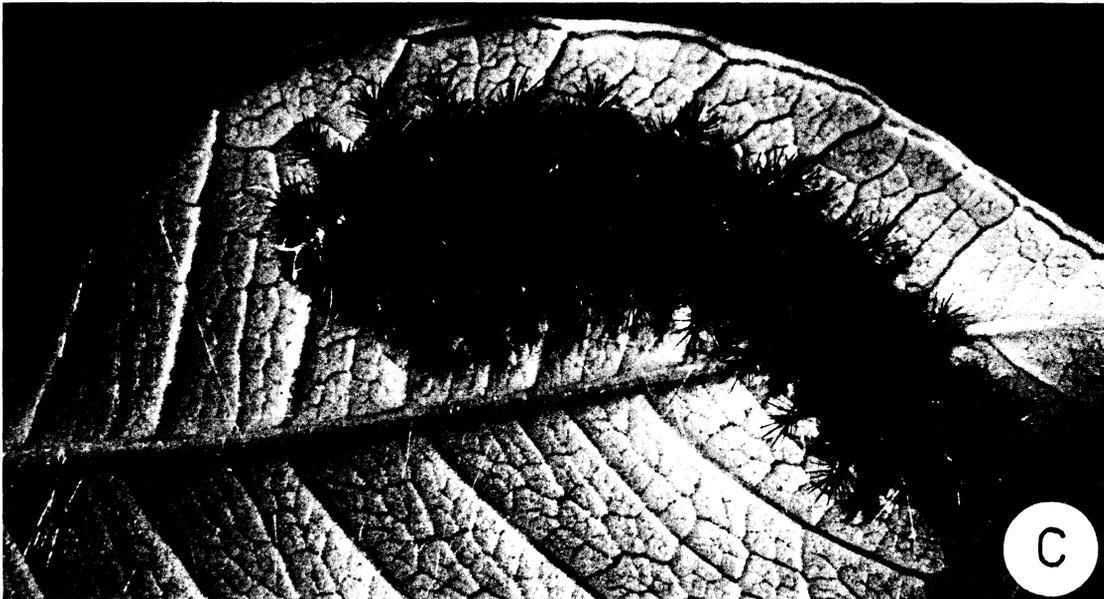
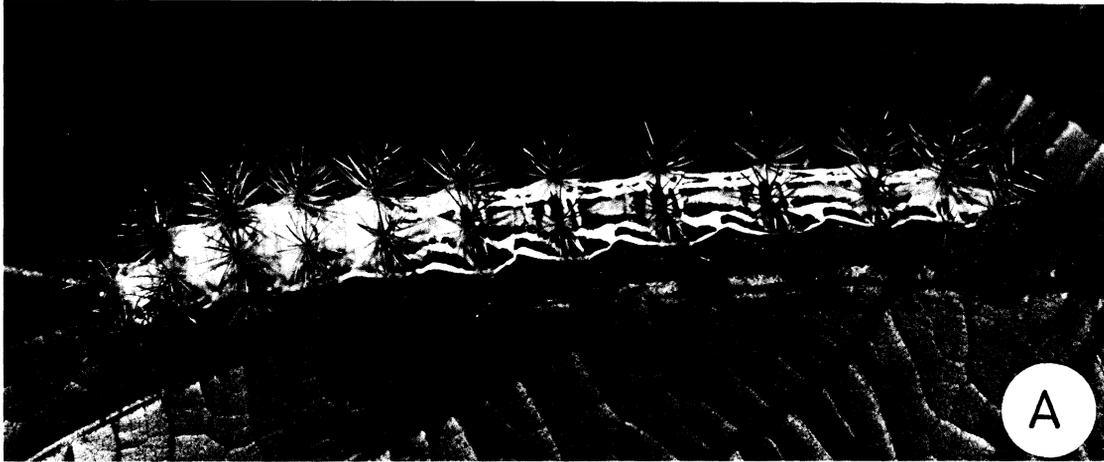
THE CATERPILLAR'S VIEWPOINT

Most Santa Rosa caterpillars occur at such low density relative to their food that there appears to be little opportunity for direct, one-on-one interactions with other caterpillars over food. However, caterpillars can and will interact indirectly in a number of ways through the medium of the resource budget of a host plant (Janzen 1973) and through carnivores. It is through such processes that a caterpillar perceives the caterpillar fauna of Santa Rosa.

CARNIVORE SHARING.—As mentioned earlier, an outbreak of one or a few species of caterpillars may draw the attention of polyphagous predators away from other species. However, if some different and edible species occur in high densities for several successive years, the predator density may then be at its maximum when a year of overall low caterpillar density occurs. This will create exceptionally intense hunting pressure on the already (or usually) scarce caterpillars of other species. On a narrower time scale, the same process occurs within a single rainy season.

In the same vein, an outbreak of caterpillars may well satiate the parasitoids that can use that caterpillar species, but an outbreak also generates a large absolute number of parasitoids. These parasitoids will then more severely challenge subsequent low-density caterpillar generations than would be the case if the parasitoid density were only that which is supported by a low density of caterpillars (see Janzen 1976, 1983b for analogous examples with vertebrates). If an outbreak is quelled by a polyphagous disease (such as occurred with *H. lineata* in 1979; Janzen 1981a, 1984a), an enormous amount of inoculant is left on foliage, branches, and the ground; redistributed later in the year and in subsequent years through rainflow, splash, and wind, the infective stages may attenuate the multispecific effect of an outbreak for many generations.

MIMICRY.—Model and mimicry systems among caterpillars depend on the component caterpillar species, as well as certain traits of the predators. For example, the many species of spiny yet harmless caterpillars (Fig. 9c) are dependent on a certain background density of urticating caterpillars (Fig. 9a) for effectiveness of their mimetic



defenses. However, this may not be true (in ecological time) for the caterpillars that depend on their possession of a color pattern (Fig. 8) that is genetically frightening to the predator (e.g., Smith 1975, 1977).

RESOURCE AND DEFENSE BUDGET.—Each time a plant is defoliated, the allocation schedules (and quantities of harvestable resource) of the plant are changed. On the one hand, such changes will affect other species of caterpillars that are using subsequent products such as leaves, shoot tips, flowers, fruits, and seeds. Defoliated trees in Santa Rosa commonly abort or otherwise fail to produce their flower or fruit crop in the subsequent sexual cycle; for example, the *Randia* spp. defoliated by *A. titan* (Janzen 1985a) bore no fruits in the rainy season following the defoliation. The fact that many Santa Rosa trees do not produce a new leaf crop until months after defoliation must also affect the other members of a tree's herbivore load. For example, when the Santa Rosa *Tabebuia ochracea* lost their entire leaf crop to the leaf-mining larvae of a chrysomelid beetle at the beginning of the 1984 rainy season, *T. ochracea* trees of all sizes did not produce new leaves until the beginning of the 1985 rainy season—a year later.

On the other hand, the interaction of Santa Rosa's plants and caterpillars may well lack the induced defenses that appear to be a major aspect of caterpillar-plant interactions in extratropical forests. I have reared batches of monophagous larvae many times on enclosed or exposed foliage that has been subject to repeated defoliation; in such rearings there is no suggestion that the regrowth foliage is any less suitable as food than was the original crop of leaves. In fact, chemical changes following defoliation are not expected in a system in which, because of carnivores, seasons, migratory behavior, etc., Lepidoptera populations do not build up on a particular tree during subsequent generations.

PARASITOID SPECIES RICHNESS.—Because there are many species of caterpillars at Santa Rosa, it is tempting to suggest that at any one season or year, at least one host species may be sufficiently abundant to sustain a somewhat polyphagous parasitoid; that is, the more life forms and species of caterpillars in a habitat, the greater the likelihood

that a particular environmental event will favor one or more of them. In this sense, it matters to a caterpillar species how many other species of caterpillars are in the habitat, even if they feed on other species of plants.

On the other hand, a habitat that is species-poor in caterpillars may average a higher caterpillar biomass per species than does a habitat that is species-rich in caterpillars. Both habitats may therefore sustain about the same species richness of caterpillar parasitoids; indeed, parasitoid species richness does not attain its highest levels in the species-rich lowland tropical forests (Janzen 1981b). The relatively low species richness of Santa Rosa tachinids and ichneumonids (M. Wood, I. Gauld, and H. Townes, pers. comm., after examining many years of rearings and malaise trap material) suggest that the increase in caterpillar species richness from, for example, Ithaca to Santa Rosa (Table 1) has not led to a concomitant increase in parasitoid species richness; that is, whether it matters to a particular species of sphingid caterpillar in Santa Rosa to co-occur with 3, 5, or 20 other species of sphingid caterpillars will depend primarily on how the carnivores view this gradient.

CONCLUSIONS

The emerging image of the Santa Rosa caterpillar fauna differs from that of extratropical caterpillar faunas in a number of ways that will probably be important in understanding how the Santa Rosa caterpillar fauna interacts with its hosts and its carnivores. On the other hand, to view the Santa Rosa caterpillar fauna as representative of the "tropics" would be a serious error: for example, the Santa Rosa caterpillar fauna differs in many major ways not herein discussed from that of other wetter and/or colder habitats only a few tens of kilometers from Santa Rosa.

It will be more years before a thorough image of Santa Rosa's caterpillar fauna is available. In the meantime, however, a simultaneous long-term intensive look at other tropical caterpillar faunas in the same and different habitats could be conducted profitably by other people. It is only through an intensive understanding of a variety of tropical habitats that we will be able both to manipulate them and to display them in such a manner as to attract public interest for their survival. There is a lot more to

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FIGURE 9. (A) Penultimate instar caterpillar of *Automeris zugana* (Saturniidae), a severely urticating caterpillar that is part of the model complex for a species-rich array of mimics of urticating caterpillars. It is green with a red head capsule and red and white markings laterally and ventrally (host plant: *Annona purpurea*, Annonaceae). (B) Last instar caterpillar of a megalopygid moth, a strongly urticating caterpillar that is part of the model complex of urticating caterpillars. It is black with white spots and densely covered with long silky orange hairs (host plant: *Enterolobium cyclocarpum*, Leguminosae; see Fig. 3C). (C) Last instar caterpillar of *Emesis mandora* (Riodinidae). This butterfly caterpillar is brilliant red with black spines and a black head capsule with white markings. It is a harmless mimic of urticating caterpillars.

the tropics than macaws in rain forest trees and lions in game parks. If we expect people to see the beauty and intrigue in the smaller world of caterpillars, then we have to learn enough about them to tell their stories.

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ERRATA

- L. P. Brower, B. E. Horner, M. A. Marty, C. M. Moffitt, and B. Villa-R, "Mice (*Peromyscus maniculatus*, *P. spicilegus*, and *Microtus mexicanus*) as predators of overwintering monarch butterflies (*Danaus plexippus*) in Mexico," *Biotropica* 17(2): 89-99. Specimens identified as *Peromyscus maniculatus* and *P. spicilegus* have been reidentified as *Peromyscus melanotis* J. A. Allen and Chapman and *Neotomodon alstoni* Merriam, respectively. For re-checking these identifications we are indebted to Drs. M. D. Carleton, G. G. Musser, and M. Engstrom.