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A Host Plant Is More Than Its Chemistry

Daniel H. Janzen

Field naturalists frequently observe that the intensity of insect herbivory in a natural defoliation event is not spread uniformly over individual conspecific plants and may even vary within one plant crown. Until the early 1960's, the general explanation would have been that heterogeneity in physical conditions, carnivory, and/or the arrival of the herbivores generate such lack of uniformity. During the past 20 years, much research on the chemical defenses of plants has paved the way for the now commonplace concept that such heterogeneity of herbivory in a defoliation event may also be caused by heterogeneity in the nutrient or defense properties of plants or plant parts (e.g., Kogan 1977). Indeed, a number of studies have found this to be the case. For example, squirrels browse much more heavily on terpene-poor ponderosa pines than on their more terpene-rich conspecifics a few meters away (Farantinos et al. 1981). Panamanian forest insects browse young leaves more intensely than they do conspecific old ones, presumably because of the greater nutrient value and lesser toughness of the former (Coley 1982, 1983a, b). Chrysomelid beetles and Finnish caterpillars vary their feeding patterns in response to seasonal changes in host leaf chemistry (Hare 1983; Haukioja & Niemela 1979).

What I would like to do in this essay is to give the pendulum a push back toward a middle ground, reminding all of us (including me) that when a herbivore moves onto a host plant it gets the outside of the plant as well as what is inside. Such integrative studies are now beginning to appear in the literature (e.g., Abrahamson et al. 1983; Coley 1982, 1983a, ~~b;~~ Connor et al. 1983; Haukioja 1980; Heinrich & Collins 1983; Kareiva 1982; Lawton 1983; McClure 1983; Niemela et al. 1982; Price et al. 1980; Rausher & Papaj 1983; Schultz 1983; Schultz et al. 1982; Stanton 1982; Thompson 1983; Washburn & Cornell 1981; Wint 1983). I feel that the philosophy that generates them deserves maximum encouragement.

I have two practical reasons for attempting this leavening, though I am sure that the reader will think of others. First, one has only so much time and resource to expend on a given study of the intensity of herbivory, and there is a very real question of whether efforts should be focused on determining the (potential) internal plant properties that drive the system or on designing observations and experiments to reveal the external factors crashing down on the lowly caterpillar. Second, in attempting to understand the ecological and evolutionary distribution of herbivores among their host plants, it is easy to forget that what might be termed the carnivory regime and climate regime of a host plant individual or population are as much traits of a plant as is its chemical profile. Both of these regimes should count for much in whether and to what degree a plant or plant part is a suitable host. When we ask why a caterpillar feeds on only one particular host species, it may be as much that it is highly adapted to the predator risks and desiccation regimes of that plant as that it is adapted to the plant's internal chemistry. By the same token, when we ask what does a herbivorous generalist have to do to be a generalist, it may be as much that it has to be able to withstand the predation risks of living on various kinds of backgrounds (e.g., Heinrich & Collins

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Randia karstenii is not correctly applied here; replace it with Randia aculeata L.

1983) as to have the gut chemistry to tolerate various kinds of food (e.g., Ahmad 1983). Which ability came first may be lost in the decomposed pages of time.

I also have an apologetic reason for attempting to meld two sequential fashions. I think we erred in not recognizing two blended questions in the seminal essay that argued that since the herbivores did not eat the green world to the ground, or even down very much, they must be regulated by the carnivores (Hairston et al. 1960). Question one is why don't all the herbivores eat up all the plants? The answer that lay undiscussed by Hairston et al. (1960) is that most of the green world is inedible to any given species of herbivore. Also lying dormant was the derivative evolutionary question of why doesn't any given herbivore species evolve the ability to eat many kinds of plants? Question two is the real question in Hairston et al. (1960); why don't the herbivores that can readily and with impunity consume a species of host plant eat their host to oblivion? Every plant species has at least one herbivore that can eat it. To some degree a plant's herbivores do consume it, thereby leaving resources for other plant species, but to a large degree they do not, with the consequence that competition and the physical environment determine much of the structure of vegetation arrays. The very same carnivory and climatic regimes that prevent herbivores from eating their hosts to oblivion are also the traits of the potential new host that must be overcome when a herbivore evolutionarily moves to, or incorporates, a new host.

Nothing I have said is new, but I feel that the emphasis is different from that of contemporary ecology and evolutionary biology; this emphasis may be witnessed in two recent books on coevolution (Futuyma & Slatkin 1983; Nitecki 1983). Virtually no attention is given to this subject, while the coevolution of herbivores and plant chemistry plays a prominent role in examples and in generation of theory.

I have chosen briefly to describe four systems as illustrative case histories rather than to dwell on hypothetical structure. I do this because of my opinion that theory in evolutionary ecology is intrinsically prone to outrun description of what is actually happening out there.

THE ARENA

The attitudes and examples in this essay derive from my experiences with the herbivore array of a lowland tropical forest, that of Santa Rosa National Park, in northwestern Guanacaste Province, Costa Rica (this site is described in detail in Janzen 1983a and in Boza & Mendoza 1981). This mosaic of deciduous forest, evergreen forest, semi-evergreen forest, and pastures regenerating to forests occupies about 11,000 ha from 0 to 350 m elevation between the Pan-American Highway and the Pacific Ocean. The area has a 5–6-month dry season (approximately December through April), and 1,000–2,000 mm of rain falls during the remainder of the year. Portions of the park were an operating cattle ranch from no later than 1710 to 1978. The vegetation contains at least 680 species broadleafed plants (at least 400 species of perennial woody plants) and supports at least 3,000 species of caterpillars plus several hundred species of other animals that eat living plant parts. There are checklists of plants (Janzen & Liesner 1980), birds (Stiles 1983), reptiles and amphibians (Scott et al. 1983), mammals (Wilson 1983), and butterflies (DeVries 1983) for the park. The plant distributions within this vegetation range from nearly monospecific stands of very large trees (e.g., 10–20-m-tall stands of *Quercus oleoides* Cham. and Schlecht., *Hymenaea courbaril* L., *Ateleia herbert-smithii* (Pittier) to highly mixed vegetation where as many as 200 species of woody plants may occur in 100 ha and adult conspecific crowns are usually separated by one to many allospecific crowns. At Santa Rosa, herbivory by caterpillars, the focus of this essay, is characteristically highly heterogeneous among years and among individuals, species, and age classes of plants (e.g., Janzen 1981).

ANATOMY OF A DEFOLIATION EVENT

The event

During the 1983 rainy season, a representative defoliation event occurred at Santa Rosa. The impact of the herbivores was highly heterogeneous. I briefly describe the ecology of this impact as an example of a pattern that could have been generated either by the heterogeneity of internal plant chemistry or by mortality factors external to the plant (or both). In fact, the pattern seems to have been generated by external factors and therefore provides an example for the introductory comments of this essay. It is described in more detail elsewhere (Janzen unpublished manuscript). While the study was conducted in a patch of Santa Rosa forest of approximately 2 km^2 (Bosque San Emilio, approximately 2 km northeast of the park administration area), the 11,000-ha park contains tens of square kilometers of this type of forest. Cursory examination of other forest patches showed that the events described here occurred at those sites as well.

The first generation

From 28 May to 4 June 1983, when 50–90-year-old secondary successional deciduous forest at Santa Rosa was just beginning budbreak following the first significant rains of the rainy season, the forest was sprinkled with ovipositing *Aellopos titan* (Cram.). One or more of these small diurnal sphingid moths (Haber & Frankie 1983) could be seen by simply standing and looking through the forest for 5 minutes or less at any time during daylight hours. The moths darted among the shrubs and treelets at a height of about 1–3 m. They touched branchlets, twigs, and buds with legs and the tip of the abdomen. Upon encountering a plant of *Randia karstenii* Polak or *R. subcordata* (Stand.) Standley, the moth hesitated a moment longer and sometimes laid a single spherical pale green egg on the bud, newly expanding leaf, thorn, or twig it contacted (Fig. 1). It then flew to other branches of the same plant or, about equally frequently, off to neighboring plants. Both species of *Randia* were beginning budbreak; a few individuals were covered with a thin layer of newly expanding leaves, while others had only swelling buds. The outcome of this oviposition, by what must have been several thousand moths in the study area, was the deposition of tens of eggs to a thousand or more eggs on each *Randia* in the forest (of 214 plants briefly examined, all had some eggs).

For example, on 5 June, all or a major portion of the potential oviposition sites on 14, 1.5–5-m-tall *R. subcordata* were searched thoroughly for *A. titan* eggs. As many as 10 eggs had accumulated on some branch ends (Fig. 1C), but 1 or 2 per branch end or bud was more usual (Fig. 1A, B). The estimated or actual numbers of eggs on these plants ranged from 21 to 1,212, with an average of 197 (SD = 316). Smaller plants (0.7–1.4 m in height) had 1–19 eggs on them ($\bar{x}$ = 6.0, SD = 5.1, *n* = 10). The small plants were not only shorter, but also had only one or a few stems and branchlets. While I did not count them, the numbers of *A. titan* eggs on the *R. karstenii* appeared to be about the same. Each hectare of this 2-km^2 patch of forest contains at least four individuals of these two *Randia* species that are 1.5 m or more in height, which allows a rough estimate of 800 oviposition plants carrying a minimum of about 160,000 *A. titan* eggs. If I assume that each female can lay 100 eggs, these eggs represent the oviposition by 1,600 moths.

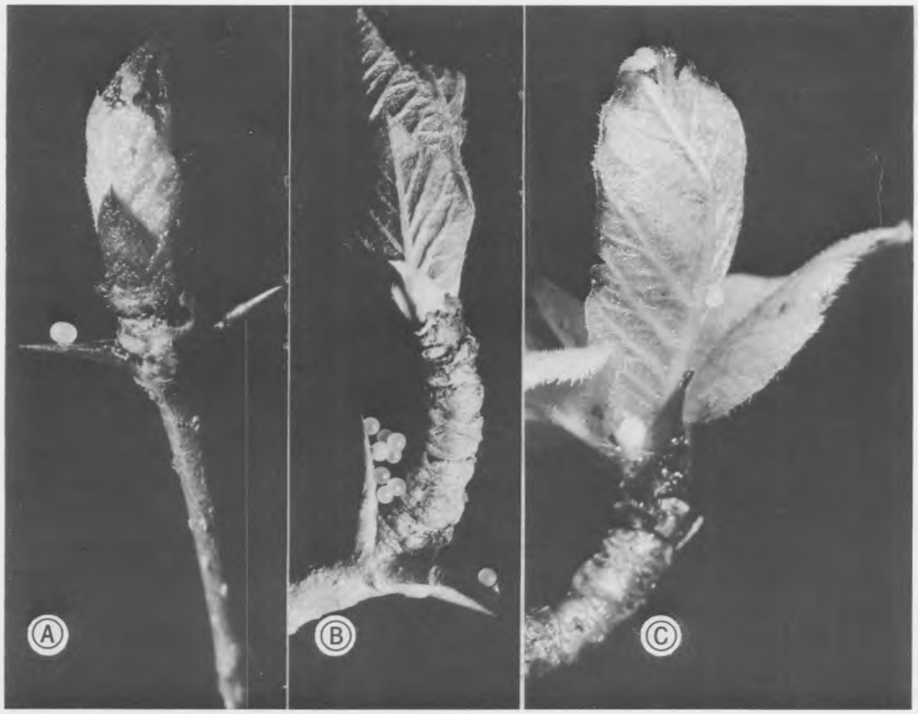

Fig. 1. — (A) Egg of *Aellopos titan* laid on a spine of *Randia subcordata* at the time of budbreak. (B) Accumulated eggs of *A. titan* following multiple ovipositions over several days on *R. subcordata*. (C) Egg of *A. titan* laid on the underside of an expanding new leaf of *R. subcordata*. 30 May 1983, Santa Rosa National Park, Costa Rica.

From the outset, the number of eggs present on a given plant was the product of several processes. Even while females were ovipositing, eggs were being carried off by *Pseudomyrmex*, *Azteca*, *Crematogaster*, and other ants, picked off by warbler-sized and -shaped birds, and fed on by anthocorid bugs. The eggs hatched 5–6 days after oviposition; even as the first were hatching, more were still being laid. While minute parasitic Hymenoptera were observed ovipositing in the eggs in the field, no parasitoids were reared from a sample of 682 eggs collected from 24 different *R. subcordata* plants, and no parasitoids appeared when 100 of these eggs were reared to the adult stage.

The first-instar larvae are pale green, match well the color of the newly expanding *Randia* leaves, and wander widely through the foliage of the plant on which they hatch. They appear to be highly edible to the ants and birds mentioned above, reduviid bugs, *Polistes* wasps, other wasps, small spiders, and carabid beetles; all of these animals were observed to capture and eat them or carry them off on numerous occasions. By 4–7 June, tens to hundreds of first- or second-instar *A. titan* larvae could be found on any *Randia* more than 1 m tall, and some larvae were present even on plants as small as 30 cm in height. On all plants the larvae appeared to be healthy and were feeding heavily.

I was absent from the site 8–13 June, and upon my return, it was evident that the outbreak had developed to the extent that three levels of defoliation could be recognized among both species of *Randia*. There were plants with only a few larvae (1–10 per plant by quick inspection), plants with moderate numbers of larvae (10–30 per plant), and plants with hundreds of larvae. On all plants, the larvae appeared to be healthy and to have about the same size distribution. On 18–20 June, 49 *R. subcordata* plants were thoroughly searched at night for larvae. By searching at night with a strong flashlight, at least 99 percent of the larvae present on a plant were located. By these dates, virtually the entire population was in the ultimate (Fig. 2) or penultimate instar. A few larvae had already left their host plants to pupate or, if the host was defoliated, to search for more food. No larvae were on 43 percent of the plants, and all of these plants showed minor defoliation; however, there was enough defoliation to make it clear that some *A. titan* caterpillars had developed to moderate size on these plants before leaving or being preyed upon. The plants (33 percent) with 1–10 larvae had either moderate defoliation (10–50 percent of their leaf

Fig. 2. — (A) Ultimate-instar caterpillar of *Aellopos titan*; this green morph has a white lateral posterior diagonal stripe and light lateral diagonal white and magenta side stripes; it is the most common morph. (B) Ultimate-instar caterpillar of *A. titan*; this dark morph is dorsally lavender and ventrally black, with white lateral markings. It is the rare morph except during crowding, heavy shading, or total defoliation. The previous two instars of *A. titan* are extremely similar to these caterpillars. 20 June 1983, Santa Rosa National Park, Costa Rica.

surface area) or total leaf loss. In the latter case, the larvae present were wandering over the surface of the plant eating off petioles, leaf blade fragments, and buds. They were obviously a small remnant of much greater numbers of larvae on the tree. Finally, there were trees (25 percent) with 11 to several hundred larvae. For example, I counted, by removal sampling, 246 last-instar caterpillars from one *R. subcordata*, and there were at least another 200 on the tree (Fig. 3). At the time of the census, these densely populated trees still had 10–30 percent of their leaf surface remaining; however, within 5 days, when all larvae had been preyed upon or had left the tree to pupate, all of these leaves had been eaten. Such trees appeared to have had caterpillars that were slightly delayed in their development or initially to have had fewer caterpillars on them than those already stripped of their leaves had had. It was evident that complete defoliation (Fig. 3, 4) was a function of the number of caterpillars on a plant and the size of the plant. Part of the heterogeneity of defoliation was generated purely by this interaction.

The large ultimate- and penultimate-instar larvae (Fig. 2), were eaten by small to medium-sized birds, reduviid bugs, scorpions, and unidentified mammals. One mammal scat, of a size that could have been produced by a gray fox, small cat, or procyonid, contained 26 head capsules of penultimate and ultimate instar *A. titan* larvae. While such an enormous population of moth larvae would seem to be an easy substrate for intense parasitization, of 617 ultimate and penultimate instar larvae collected and reared, only seven caterpillars were parasitized by tachinids, and none contained parasitic Hymenoptera (Table 1).

The prepupal wandering stage of *A. titan* walks or drops off a plant and burrows into the litter to pupate. Of those which pupated in captivity, all living individuals emerged from the pupal

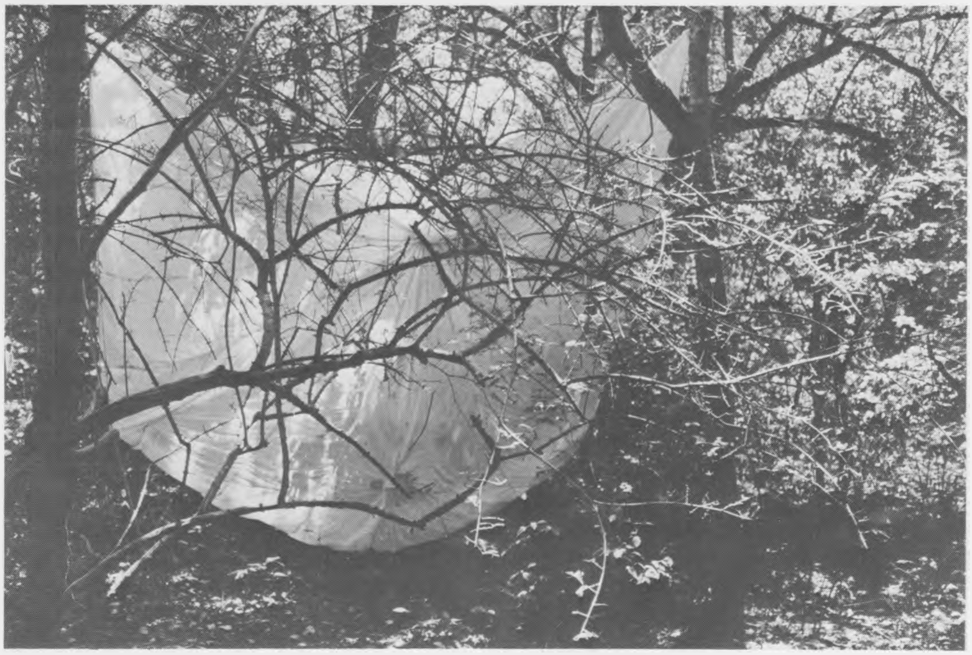

Fig. 3. — *Randia subcordata* adult tree defoliated by *Aellopos titan*; 3 days before this photograph was taken, this tree had at least 446 ultimate-instar *A. titan* caterpillars on it. The top of the parachute background is 3.8 m above the ground at each end. 23 June 1983, Santa Rosa National Park, Costa Rica.

Fig. 4 — *Randia karstenii* subadult treelet defoliated by *Aellopos titan*. 23 June 1983, Santa Rosa National Park, Costa Rica.

stage about 13–15 days after pupation (between 6 and 20 July). Pupal-stage duration was not influenced by wet or extremely dry conditions. The newly emerging adults simply left the site where they had developed; they were not observed at flowers that are standard nectar hosts for *Aellopos* (e.g., *Cedrela odorata* L., which were visited by hundreds of female moths at the time of oviposition in early June). Despite extensive and intensive nocturnal searches of *Randia* shrubs from mid-July to the end of August, only three *A. titan* larvae were located. There was no evidence of an attempted or realized second generation of the moth at this site or in other parts of the Santa Rosa forest.

The pupae in the litter were subject to moderate predation by vertebrates. Collared peccaries [*Tayassu tajacu* (L.)] and nine-banded armadillos (*Dasypus novemcinctus* L.) snuffled intensively through the litter below the *Randia* that had had large numbers of caterpillars, and I presume they were harvesting *A. titan* pupae. Spiny pocket mice [*Liomys salvini* (Thomas)] ate the pupae readily in the laboratory and foraged incessantly at night in the forest litter for seeds and insect pupae; on one occasion a mouse brought an *A. titan* pupa into a live trap and ate part of it there. However, living *A. titan* pupae could easily be found by sorting through litter until the time of adult eclosion in mid-July, and numerous newly eclosed adults were encountered on the foliage at that time. There is no doubt that despite the various sources of mortality mentioned above and later, a large number of adults eclosed in Bosque San Emilio and in other patches of deciduous forest in Santa Rosa.

Two weeks after the *A. titan* larvae had disappeared from the *Randia*, I walked a line transect through the Bosque San Emilio and estimated the intensity of defoliation of all *Randia* encountered (14 July 1983). Of 173 *R.*

Table 1. — Fate of 617 penultimate and ultimate instar *Aellopos titan* larvae collected from *Randia subcordata* and *R. karstenii* in Bosque San Emilio, Santa Rosa National Park, Costa Rica (1983).

Date and Host	(n)	Percent Eclosed	Killed by Disease			Parasitized Larvae
			As Larvae	As Pupae	Total	
18 June *R. s.*	(109)	60	15	26	41	0
18 June *R. k.*	(117)	60	17	21	38	1
19 June *R. s.*	(234)	42	28	28	56	3
20 June *R. s.*	(79)	82	4	14	18	3
23 June *R. s.*	(50)	90	0	10	10	0
24 June *R. k.*	(28)	93	0	7	7	0

subcordata, 41 percent were leafless (Fig. 3), 28 percent were moderately but conspicuously defoliated (often with one part of the crown more severely defoliated than another), and the remainder (31 percent) showed only traces of the feeding damage characteristic of *A. titan* larvae. Of 181 *R. karstenii* encountered, 63 percent were essentially leafless (Fig. 4), 30 percent were moderately defoliated, and the remainder appeared intact but had probably been fed on. Since *R. karstenii* leaves are very small and have a weak midrib, the larvae generally ate the entire leaf; small amounts of damage were therefore harder to recognize than they were on *R. cordata*. By the last half of August, all of the defoliated plants were putting out a new leaf crop and appeared approximately as they did during the first week of June. On 15 June 1983, a transect of forest along Quebrada Costa Rica (about 5 km SW of Bosque San Emilio and slightly drier) located 51 *R. karstenii*. All of these plants had lost all of their leaves to *A. titan*.

During the 1979–1982 growing seasons there was no defoliation of *Randia* by *A. titan* (or by any other insect). Frequent searches of numerous *Randia* plants during these 4 years yielded eight *Aellopos* larvae from Bosque San Emilio forest, six of which were parasitized by tachinids or Hymenoptera. The enormous number of adult female *A. titan* which appeared, as if by magic, in the Santa Rosa deciduous forest 25–28 May 1983 must have come from elsewhere, and when their offspring eclosed, they went elsewhere. Whether they arrived as a consequence of having concentrated in a large down-wind area in response to the odor of newly foliating *Randia*, or whether some more complex congregation event occurred, is beyond the scope of this essay.

My field notes from the 1978 rainy season suggest that there was a high density of *A. titan* on *Randia* in the Bosque San Emilio in late May and early June. While I was not collecting caterpillars in the field at that time, other biologists brought me 23 casually encountered *A. titan* larvae from "*Randia*" in this forest.

This account suggests several questions pertinent to this essay. Why did the newly eclosed adults not attempt a second generation at Santa Rosa by ovipositing on the foliated *Randia*? Why were predation and parasitization rates not high enough to eliminate the first generation or at least depress it to the levels of the 1979–1982 rainy seasons? Why was the final result of this "outbreak" a very heterogeneously defoliated array of *Randia* trees?

No second generation

At the time of *A. titan* eclosion (early to mid-July), the undefoliated *Randia* had at least 5, perhaps 6, months of leafiness ahead of them. Since the egg-to-adult time for *A. titan* is about 35 days, there is ample time in the rainy season for at least three generations. Throughout the 1979–1982 rainy seasons, there were such generations at extremely low densities. In 1981, I recorded *A. titan* oviposition on *R. subcordata* as late in the rainy season as 10 January. In mid-August 1983, I encountered two last instar larva on *R. subcordata* and a single last instar larva on *R. karstenii*, but it was clear that no large pulse of eggs and larvae appeared on *Randia* foliage in July as it did in late May and early June.

Therefore it is clear that the newly eclosing *A. titan* females were confronted with a moderate number of leafy *Randia*, but either they rejected them as oviposition sites and went elsewhere or were programmed to leave the site irrespective of available food. Ironically, a leafy *Randia* that has escaped a defoliation event is probably an unsuitable oviposition site. If *Randia* are foliated because of leaf chemistry (unlikely; see below), then the female should not oviposit on leafy *Randia*. In contrast, until the second half of

August, defoliated individuals did not have enough leaves to support even a few caterpillars. They were leafless at the time of eclosion of the first generation. If, as I suspect, the foliated *Randia* is an indicator of high carnivory risk to eggs and caterpillars, then again, it is not a good oviposition site; the leafless *Randia* suggests a low risk site but offers no food. Selection should favor females that will ignore foliated *Randia* at the site of their birth and search in space or time for sites not subjected to recent defoliation.

It is appropriate to add here that I have observed *A. titan* females to oviposit on the new, partly expanded leaves of *R. subcordata* and *R. karstenii* during all months of the rainy season at Santa Rosa. Furthermore, I have reared their caterpillars on leaves of all ages in all months of the rainy season. While newly foliating *Randia* in late May and early June have more newly expanding leaves than at any other time, the plants also have some newly elongating branchlets at all times of the growing season. There are always some oviposition sites for *A. titan* during the rainy season in the Santa Rosa deciduous forests, even if they will only oviposit on very young foliage.

Relatively low carnivory rates

While eggs and larvae of *A. titan* suffered conspicuous and intense predation, it was not sufficient to eliminate a highly evident array of caterpillars. As a *Randia* was becoming fully defoliated, for the last 2–8 days virtually no search was necessary to see tens of *A. titan* caterpillars on its ever more naked branches and petioles. However, these plants were not being subjected to hoards of insectivorous birds, mammals, or carnivorous insects. During several hours of observing *Randia* heavily infested with ultimate and penultimate instar caterpillars, it was customary to encounter 5–10 reduviid bugs, each killing one caterpillar; several caterpillars being stung or carried off by ants; one or two being carried off by small to medium-sized birds; and several apparently starving to death because they had fallen or wandered off their host plant. Some plants clearly had all of their caterpillars removed by carnivores, while others retained large numbers even after many had been removed; however, carnivore density was simply not high enough nor their searching thorough enough to depress the *A. titan* caterpillar density on all trees to a level even approximating the low level "normally" observed.

Either the Santa Rosa carnivore density was exceptionally low in 1983 or exceptionally large numbers of *A. titan* eggs were laid there in early 1983. I have no formal census data on carnivore density at Santa Rosa in 1979–1982, but certainly the 1983 density of birds and other predators did not seem to be any lower than were the 1979–1982 levels.

I should add, incidentally, that these levels are much lower than those readily visible in, for example, a Minnesota or Michigan woodlot in late May. However, I can state that there was no massive input of *A. titan* eggs and larvae in the 1979–1982 rainy seasons.[1]

The startlingly low numbers of parasitized *A. titan* larvae (Table 1) are consistent with records for other species of caterpillars at Santa Rosa that have suddenly increased greatly in density (unpublished field records). A hypothesis consistent with this low rate of parasitization is that the enormous number of larvae satiated the ovipositional capacity of the parasitoids present. It was striking that four of the seven parasitized larvae had different species of parasitoids in them and that none of the parasitoids were species that I had reared from *A. titan* in the past.

While I could not monitor disease levels in the field, the results of rearing

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[1] Note added in press: Likewise, in the 1984 and 1985 rainy seasons at Santa Rosa there was no massive input of *A. titan*.

penultimate and ultimate instar wild-caught caterpillars show clearly that disease was taking a severe toll of the caterpillars. The 617 caterpillars collected on 18–24 June (Table 1) were placed in individual plastic bags and were fed with foliage from plants lightly to moderately defoliated by *A. titan* (no plants were available with no *A. titan* damage). The bags were new or had been used (less than 1 percent) to house pupae of undiseased Saturniidae. Overall 39 percent of the caterpillars died of an unknown disease as larvae and as pupae of all ages. By way of contrast, *Aellopos* penultimate or ultimate instar larvae collected during 1979–1982 at Santa Rosa (three species on four host plant species, *n* = 53) invariably produced either adults or parasitoids, even though they were reared in exactly the same manner. The data in Table 1 suggest that the larger the collection of caterpillars, the fewer are killed by disease. However, the relationship actually lies with the age of the caterpillars at the time of collection. The 19 June sample contained the largest number of penultimate instars and the 23 and 24 June samples contained only ultimate instars with 1–3 days remaining before pupation. In the earliest samples, there were infected caterpillars that were fated to die in nature as larvae and that then died in my rearing bags. In the latest samples, those caterpillars that were fated to die in nature as caterpillars had already done so.

It is unlikely that the *A. titan* "outbreak" escaped annihilation because the predators and parasitoids were occupied elsewhere with some other species of prey. The overall caterpillar density in Bosque San Emilia in 1983 was conspicuously lower than in 1979–1982. Furthermore, 5 weeks, one *A. titan* generation, is insufficient time for a functional response by the predator and parasite array. A numerical response depends on both the distance over which the carnivores must move and the areal extent of the high density of prey. Little can be said about either in this tropical habitat, but it was clear that the high density of *A. titan* larvae covered hundreds of hectares. Also, this part of Costa Rica is not replete with large numbers of, for example, small insectivorous birds that could or would move to an "outbreak" of this sort.

In short, it appears that the local carnivores did not eliminate the *A. titan* outbreak because there were not enough of them to do so. I suspect that this was the case because (1) the outbreak occurred during the first weeks of the rainy season before whatever seasonal increase in carnivores that might occur had occurred, and (2) the habitat is not rich enough in prey to maintain a sufficiently high level of carnivores that they could consume a prey pulse with the properties of the *A. titan* caterpillars. Such an answer contains the implicit assumption that *A. titan* caterpillars are not suitable or available prey to a moderately large portion of the diverse carnivore array at Santa Rosa. The reasons range from physiological incompatibility to size and behavior. For example, the *Enicospilus* (Ichneumonidae) parasitoids that were heavily parasitizing large *Rothschildia lebeau* (Guer.-Meneville) (Saturniidae) larvae at the same time in the same forest, have never been encountered in over a thousand rearings of *Aellopos* and other Sphingidae caterpillars in Santa Rosa. The *Pseudomyrmex* and *Azteca* ants that so eagerly kill and carry off first and second instar *A. titan* larvae show no attack response to penultimate and ultimate instar *A. titan* larvae. Coatis [*Nasua nasua* (L.)] readily eat the larvae but do not readily climb the very thin and spiny branches of *Randia*. White-faced monkeys [*Cebus capucinus* (L.)] generally do not forage as low as 1–3 m above the ground in the forest interior during the rainy season and might well have never noticed the outbreak going on below them. The few species of North American migrant birds that visit Guanacaste during the northern winters had long since departed (see Janzen 1980).

Heterogeneous defoliation

The array of predators in a tropical forest possesses sufficient patterned variation in its foraging to generate heterogeneous defoliation from an initial high level and thoroughly spread layer of eggs and caterpillars. One *Randia* may be close to and foraged extensively on by a colony of *Azteca* or *Camponotus* ants, and another only a few meters away may only be passed through by an occasional far-wandering *Pseudomyrmex* ant. A *Campylorhynchus* wren family may have only a single *Randia* in its foraging territory and may therefore thoroughly glean it of its caterpillars; another wren family may have 20 *Randia* in its territory and therefore only moderately glean several and ignore the remainder (F. Joyce, Division of Ecology and Systematics, Cornell University, personal communication). A reduviid bug that settles on a small *Randia* with 10 half-grown caterpillars may well kill all of them before they have done serious defoliation; the same bug on a neighboring tree with 30 caterpillars will at best only slow the time to total defoliation by a few days, since the surviving 20 caterpillars will be quite enough to eat all the leaves off the tree. Had only a few *A. titan* eggs been laid in the forest (as in 1979–1982), heterogeneity of predation would still have occurred, but the consequence would have been invisible against the background of the initial heterogeneity of oviposition. Had there been no carnivory in 1983, all the leaves would have been eaten off all the *Randia* trees, and there would have been major *A. titan* death by starvation. It can be argued that the failure of females to avoid previously laid eggs when ovipositing may well be due to the absence of selection for such behavior if it is usual for the number of surviving offspring to be unrelated to the number of offspring initially present on the plant. Her best chance is to distribute her eggs thinly over the *Randia* population, thereby maximizing the chance of placing some eggs on those *Randia* where there is low risk from predators.

The strong heterogeneity of defoliation could, at least in theory, also have been generated by heterogeneity in the suitability of the *Randia* foliage in terms of nutrients and secondary chemical defenses. Numerous natural history facts and suppositions argue against this possibility:

1. When second- to fifth-instar larvae were removed from *Randia* that they had defoliated and then were placed on *Randia* that had lost their initial caterpillars, they fed, developed, and pupated normally whether this was done in the field (under a protective net) or in plastic bags in the laboratory. In the laboratory, all larvae produced adults that were smaller than wild adults. However, they were equally dwarfed if they were fed leaves from their partly defoliated tree or leaves from trees quite free from damage (i.e., living in a plastic bag is suboptimal).

2. Defoliation was a function of tree size as well as of caterpillar numbers. A representative 2-m tall tree with 30 developing middle-sized larvae on it was defoliated by the time they left the tree to pupate; a 4-m tall tree with the same number of larvae suffered only minor damage, since it had many more leaves than did the smaller tree.

3. At least 40 different and foliated *Randia subcordata* trees were defoliated by harvesting their leaves to feed larvae in the laboratory. These larvae all developed normally with virtually no death except by disease, parasitoids, and laboratory accidents; their development time was not longer than that of their siblings left on *Randia* in the forest.

4. All foliated trees were fed on to some degree, and a careful search of many trees with no conspicuous damage revealed that one to five large and healthy caterpillars were feeding on them. When the foliage from these

trees was offered to second-instar larvae in the laboratory, these larvae fed readily and developed into normal adults.

It is tempting to wish that one could a priori know which trees were to be defoliated and therefore could obtain a leaf sample whose chemistry could be compared with those of leaves from trees not defoliated. However, this procedure was, and is, impossible when the moth has only one defoliating generation at a site in a season. Furthermore, all *Randia* individuals were fed on by at least one or more caterpillars; defoliation was a matter of degree. Finally, there is the problem of knowing what chemicals to search for in such a comparison. It might well turn out that the eventually defoliated trees would be found to differ chemically from those that were not defoliated. However, there would be no reason to believe that these particular chemical differences, rather than some other covarying plant traits, were responsible for the final levels of defoliation.

HETEROGENEITY AMONG LIFE FORMS AND HABITATS

The risk of carnivory is important to caterpillars (e.g., Heinrich & Collins 1983; Holmes et al. 1979). This risk is not uniformly distributed among plant life forms (e.g., Thompson 1983; Royama 1970; Niemela et al. 1982) nor among the habitat types associated with different life forms. For example, a single large caterpillar in the crown of a large tree that projects above the vegetation should have a quite different probability of being located by a bird than if it were in the crown of a small sapling of the same species of tree projecting from young secondary succession. Likewise, a caterpillar in prey-rich, forest-edge herbaceous vegetation is more likely to be encountered by a *Polistes* wasp than if it were in the prey-poor canopy of a patch of evergreen forest. At Santa Rosa, the distribution of saturniid and sphingid caterpillars among their host plants provides an example.

At Santa Rosa, there are 30 breeding populations of Saturniidae (Janzen 1982) and at least 63 breeding populations of Sphingidae (Janzen 1984b). In an ongoing study, I have located at least one native host plant for 80 percent of the saturniids and 77 percent of the sphingids known or strongly suspected to breed at Santa Rosa (Tables 2 and 3). After examining only the host Latin binomials and caterpillar family names in Tables 2 and 3, it is evident that the huge caterpillars of sphingids and saturniids have little in common in their use of food plants (Janzen 1984b). Furthermore, at least half of the overlap in the two lists is a more apparent than a real similarity of food choice.

In keeping with current emphases on the causes of host specificity, several years ago a slightly reduced subset of the plants in Tables 2 and 3 was analyzed for phenolics and alkaloids (Janzen & Waterman 1983). The foliage of the saturniid hosts was found to contain significantly more phenolics and less water than did that of the sphingid hosts, while the sphingid hosts much more frequently contained alkaloids than did the saturniid hosts. These results are in strong agreement with two general impressions held by lepidopterists: (1) Most saturniids feed on tree foliage (traditionally viewed as rich in tannins), and (2) most sphingids feed on plants in families famous for toxic small molecules, resins, and copious latex flow. While not meaning to denigrate the reality of these patterns, there is obviously a quite different way to view the same set of host records.

It is evident that, as found in nature, the saturniid caterpillars are generally in the crowns of adult trees, while the sphingid caterpillars are found in plants ranging from small herbs to vines to saplings to crowns of large trees (Tables 2 and 3). The most

Table 2. — Larval hosts of Saturniidae in nature in Santa Rosa National Park, Costa Rica (as of December 1983).

Larva	Host	Microhabitat
Arsenurinae		
Arsenura armida (Cram.)	*Bombacopsis quinatum* (Jacq.) Dugand (Bombacaceae)	large tree crown
Caio championi (Drc.)	*Bombacopsis quinatum* (Jacq.) Dugand (Bombacaceae)	large tree crown
Copiopteryx semiramis (Cram.)	*Manilkara chicle* (Pittier) Gilly (Sapotaceae)	large tree crown
Dysdaemonia boreas (Cram.)	*Ceiba pentandra* (L.) Gaerth. (Bombacaceae) [a]	large tree crown
Titaea tamerlan (Maassen)	*Bombacopsis quinatum* (Jacq.) Dugand (Bombacaceae)	large tree crown
Ceratocampinae		
Adeloneivaia isara (Dognin)	*Lysiloma divariciata* (Jacq.) Macbride (Leguminosae)	large tree crown
	Lysiloma auritum (Schl.) Benth. (Leguminosae)	large tree crown
Citheronia bellavista (Draudt)	*Phoradendron quadrangulare* (HBK) Krug & Urb. (Loranthaceae) [b]	parasite in crown of large tree
Citheronia lobesis (W. Rothschild)	*Cochlosperum vitifolium* (Willd.) Spreng. (Cochlospermaceae)	large saplings
	Bursera simaruba (L.) Sarg. (Burseraceae)	large tree crown
	Spondias mombin L. (Anacardiaceae)	large saplings
	Psidium guajava L. (Myrtaceae) [c]	shrubby treelet
	Calycophyllum candidissimum (Vahl.) DC. (Rubiaceae)	large tree crown
	Phoradendron quadrangulare (HBK.) Krug & Urb. (Loranthaceae)	parasite in crown of large tree
Eacles imperialis (Dry.)	*Cochlospermum vitifolium* (Willd.) Spreng. (Cochlospermaceae)	large saplings and large tree crown
	Bursera tomentosa (Jacq.) Triana & Planch. (Burseraceae)	large tree crown
	Astronium graveolens Jacq. (Anacardiaceae)	large tree crown
	Cedrela odorata L. (Meliaceae)	large tree crown
Othorene purpurascens (Schaus)	*Manilkara chicle* Pittier (Gilly) Sapotaceae	large tree crown
Othorene verana (Schaus)	*Quercus oleoides* Cham. & Schlecht. (Fagaceae)	large tree crown
Ptiloscola dargei Lemaire	*Acacia tenuifolia* (L.) Willd. (Leguminosae)	saplings and large vine crown
Schausiella santarosensis Lemaire	*Hymenaea courbaril* L. (Leguminosae)	large tree crown
Syssphinx colla (Dyar)	*Pithecellobium saman* (Jacq.) Benth. (Leguminosae)	large tree crown
Syssphinx mexicana (Bdv.)	*Acacia collinsii* Safford (Leguminosae)	sapling to adult treelet crown
	Acacia cornigera L. (Leguminosae)	sapling to adult treelet crown

Table 2. — Continued

Larva	Host	Microhabitat
Syssphinx molina (Cram.)	*Pithecellobium saman* (Jacq.) Benth. (Leguminosae)	large tree crown
	Cassia grandis L. (Leguminosae) [c]	large tree crown
	Albizzia adinocephala (Donn. Sm.) Britt. & Rose (Leguminosae)	large tree crown
Syssphinx quadrilineata (G. & R.)	*Pithecellobium saman* (Jacq.) Benth. (Leguminosae)	large tree crown
Hemileucinae		
Automeris io (F.)	*Crescentia alata* HBK. (Bignoniaceae) [c]	large tree crown
	Mimosa pigra L. (Leguminosae)	shrub
	Cassia biflora L. (Leguminosae)	shrub
	Rhynchosia reticulata (Swartz) DC. (Leguminosae)	herbaceous vine
	Gliricidia sepium (Jacq.) Walp. (Leguminosae)	sapling
Automeris rubrescens (Wlk.)	*Inga vera* Willd. (Leguminosae)	sapling
	Rourea glabra HBK. (Connaraceae)	scandent shurb
	Guazuma ulmifolia Lam. (Sterculiaceae)	large tree crown
	Cassia biflora L. (Leguminosae)	shrub
	Querus oleoides Cham. & Schlecht. (Fagaceae)	sapling
	Cordia alliodora (R. & P.) Oken (Boraginaceae)	sapling
	Lonchocarpus minimiflorus Donn. Smith (Leguminosae)	sapling
	Calycophyllum candidissimum (Vahl.) DC. (Rubiaceae)	large tree crown
	DHJ 12175 (Bignoniaceae)	sapling vine
	Zuelania guidonia (SW.) Britt. & Millsp. (Flacourtiaceae)	large tree crown
	Crescentia alata HBK. (Bignoniaceae) [c]	large tree crown
	Cassia grandis L. (Leguminosae)	large tree crown
Automeris zugana Drc.	*Annona purpurea* Moc. & Sesse (Annonaceae)	large tree crown
	Lonchocarpus costaricensis Pittier (Leguminosae)	large tree crown
	Querus oleoides Cham. & Schlecht. (Fagaceae)	large tree crown
	Cydista heterophylla Seib. (Bignoniaceae)	large woody vine
	Calycophyllum candidissimum (Vahl.) DC. (Rubiaceae)	sapling to large tree crown
	Hymenaea courbaril L. (Leguminosae)	sapling
	Solanum hazenii Britt. (Solanaceae)	large herb
	Lantana camara L. (Verbenaceae) [c]	large herb/shrub
	Lonchocarpus eriocarinalis Micheli (Leguminosae)	large tree crown
	Centrosema pubescens Benth. (Leguminosae)	herb vine

Table 2. — Continued

Larva	Host	Microhabitat
	Cassia hayesiana (B. & R.) Standl. (Leguminosae)	shrub/treelet
	Inga vera Willd. (Leguminosae)	sapling
	Serjania atroliniata Sauv. & Wr. (Sapindaceae)	large vine
Dirphia avia (Stoll)	*Hymenaea courbaril* L. (Leguminosae)	large tree crown
	Cedrela odorata L. (Meliaceae)	large tree crown
Hylesia dalina Schaus	*Casearia arguta* HBK. (Flacourtiaceae)	treelet
	Malvaviscus arboreus Cav. (Malvaceae)	shrub
Hylesia lineata Drc.	*Tabebuia rosea* (Vertol.) DC. (Bignoniceae)	sapling
	Bombacopsis quinatum (Jacq.) Dugand (Bombacaceae)	large tree crown
	Cordia alliodora (R. & P.) Oken (Boraginaceae)	treelet
	Hirtella racemosa Lam. (Chrysobalanaceae)	treelet
	Muntingia calabura (Swartz) DC. (Elaeocarpaceae)	treelet
	Casearia arguta HBK. (Flacourtiaceae)	treelet
	Casearia sylvestris SW. (Flacourtiaceae)	treelet
	Casearia corymbosa HBK. (Flacourtiaceae)	treelet
	Zuelania guidonia (SW.) Britt. & Millsp. (Flacourtiaceae)	large tree crown
	Acacia tenuifolia (L.) Willd. (Leguminosae)	large vine crown
	Cassia biflora L. (Leguminosae)	shrub
	Diphysa robinioides Benth. (Leguminosae)	sapling
	Enterolobium cyclocarpum (Jacq.) Griseb. (Leguminosae)	large tree crown
	Hymenaea courbaril L. (Leguminosae)	sapling
	Inga vera Willd. (Leguminosae)	treelet
	Lonchocarpus minimiflorus Donn. Smith. (Leguminosae)	treelet
	Lonchocarpus costaricensis Pittier (Leguminosae)	sapling
	Lysiloma auritum (Schl.) Benth. (Leguminosae)	large tree crown
	Machaerium kegelii (Meisner) (Leguminosae)	sapling large vine
	Mimosa pigra L. (Leguminosae)	shrub
	Myrospermum frutescens Jacq. (Leguminosae)	treelet
	Pithecellobium lanceolatum (H. & B.) Benth. (Leguminosae)	treelet
	Hyptis pectinata Poit. (Labiatae)	large herb
	Malvaviscus arboreus Cav. (Malvaceae)	shrub
	Banisteriopsis muricata (Cav.) Cuatr. (Malpighiaceae)	low vine

Table 2. — Continued

Larva	Host	Microhabitat
	Byrsonima crassifolia (L.) HBK. (Malpighiaceae)	treelet
	Stigmaphyllon ellipticum (HBK.) Adr. Juss. (Malpighiaceae)	low vine
	Psidium guineense SW. (Myrtaceae)	shrub
	Ouratea lucens (HBK.) Engler (Ochnaceae)	shrub
	Gouania polygama (Jacq.) Urban (Rhamnaceae)	low vine
	Calycophyllum candidissiumum (Vahl.) DC. (Rubiaceae)	sapling
	Chomelia spinosa Jacq. D. (Rubiaceae)	treelet
	Guettarda macrosperma D. Sm. (Rubiaceae)	treelet
	Xanthoxylum setulosum P. Wilson (Rutaceae)	sapling
	Allophyllus occidentalis (SW.) Radlk. (Sapindaceae)	treelet
	Cupania guatemalensis (Turcz.) Radlk. (Sapindaceae)	treelet
	Paullinia cururu L. (Sapindaceae)	low vine
	Serjania schiedeana Schlecht. (Sapindaceae)	low vine
	Urvillea ulmacea HBK. (Sapindaceae)	low vine
	Byttneria aculeata Jacq. (Sterculiaceae)	shrub
	Byttneria catalpaefolia Jacq. (Sterculiaceae)	low vine
	Guazuma ulmifolia Lam. (Sterculiaceae)	medium tree
	Luehea speciosa Willd. (Tilliaceae)	sapling
	Lantana camara L. (Verbenaceae)[c]	shrub
	Erythroxylum havanense Jacq. (Erythroxylaceade)	shrub
	Calliandra emarginata Benth. (Leguminosae)	shrub
Periphoba arcaei (Drc.)	*Eugenia salamensis* Donn. Sm. (Myrtaceae)	medium tree crown
	Cassia biflora L. (Leguminosae)	shrub
	Guazuma ulmifolia Lam. (Sterculiaceae)	large tree crown
	Lysiloma auritum (Schl.) Benth. (Leguminosae)	large tree crown
	Spondias mombin L. (Anacardiaceae)	large tree crown
	Rourea glabra HBK. (Connaraceae)	scandent shrub
	Annona purpurea Moc. & Sesse (Annonaceae)	treelet crown
	Calycophyllum candidissimum (Vahl.) DC. (Rubiaceae)	large tree crown
	Bombacopsis quinatum (Jacq.) Dugand (Bombacaceae)	large tree crown

Table 2. — Continued

Larva	Host	Microhabitat
	Cassia alata L. (Leguminosae)[c]	large tree crown
	Inga vera Willd. (Leguminosae)	medium tree crown
	Ardisia revoluta HBK. (Myrsinaceae)	treelet
	Astronium graveolens Jacq. (Anacardiaceae)	sapling
	Hymenaea courbaril L. (Leguminosae)	sapling
	Quercus oleoides Schlecht. & Cham. (Fagaceae)	large tree crown
	Miconia argentea (Swartz) DC. (Melastomataceae)	sapling
Saturniinae		
Copaxa moinieri Lemaire	*Ocotea veraguensis* (Meisn.) Vlez (Lauraceae)	saplings and lower branches of treelet
Rothschildia erycina (Shaw)	*Exostema mexicanum* (Jacq.) Roem. & Schult.	large tree crown
	Coutarea hexandra (Jacq.) Schum. (Rubiaceae)	treelet crown
Rothschildia lebeau (Guer.-Meneville)	*Exostema mexicanum* Jacq. Roem. & Schult. (Rubiaceae)	large tree crown
	Spondias mombin L. (Anacardiaceae)	large tree crown
	Spondias purpurea L. (Anacardiaceae)	treelet
	Casearia corymbosa HBK. (Flacourtiaceae)	treelet
	Zuelania guidonia (Sw.) Britt. & Rose (Flacourtiaceae)	large tree crown
	Xanthoxylum setulosum P. Wilson (Rutaceae)	large tree crown

[a] Not yet found in nature but accepts readily and dies on other Santa Rosa Bombacaceae.

[b] Not yet found in nature but accepts readily and has the appropriate color and behavior to use this host.

[c] Plant introduced to Santa Rosa within past several hundred years.

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Table 3. — Larval hosts of Sphingidae in nature in Santa Rosa National Park, Cost Rica (as of December 1983).

Larva	Host	Microhabitat
Aellopos clavipes (R. & J.)	*Randia karstenii* Polak (Rubiaceae)	sapling to treelet
Aellopos fadus (Cram.)	*Genipa americana* L. (Rubiaceae)	sapling to large tree
	Alibertia edulis A. Rich. (Rubiaceae)	shrub
Aellopos titan (Cram.)	*Randia karstenii* Polak (Rubiaceae)	sapling to treelet
	Randia subcordata (Stand.) Standley (Rubiaceae)	sapling to treelet
Agrius cingulatus (F.)	*Merremia umbellata* (L.) Hall (Convolvulaceae)	herb vine

Table 3. — Continued

Larva	Host	Microhabitat
	DHJ 12071 (Convolvulaceae)	herb vine
Aleuron carinata Wlk.	*Doliocarpus dentatus* (Aubl.) Stand. (Dilleniaceae)	low perennial vine
Aleuron iphis Wlk.	*Tetracera volubilis* L. (Dilleniaceae)	low perennial vine
Amplypterus gannascus (Stoll)	*Ocotea veraguensis* (Meisn.) Vlez (Lauraceae)	sapling to treelet
Amplypterus ypsilon R. & J.	*Ocotea veraguensis* (Meisn.) Vlez (Lauraceae)	sapling to treelet
Callionima falcifera (Gehlen)	*Stemmadenia obovata* (Hook & Arn.) K. Schum. (Apocynaceae)	sapling to treelet
Cautethia spuria (Bdv.)	*Exostema mexicanum* A. Gray (Rubiaceae)	sapling to large tree
	Coutarea hexandra (Jacq.) Schum. (Rubiaceae)	treelet
Cautethia yucatana B. P. Clark	*Exostema mexicanum* A. Gray (Rubiaceae)	treelet
Cocytius duponchel (Poey)	*Annona purpurea* Moc. & Sesse (Annonaceae)	sapling to treelet
	Annona reticulata L. (Annonaceae)	sapling to treelet
Enyo ocypete (L.)	*Tetracera volubilis* L. (Dilleniaceae)	low perennial vine
	Cissus rhombifolia Vahl. (Vitaceae)	herb vine
Erinnyis ello (L.)	*Sebastiana confusa* Lundell (Euphorbiaceae)	sapling to treelet
	Sapium thelocarpum Schm. & Pitt. (Euphorbiaceae)	sapling
	Manilkara chicle (Pittier) Gilly (Sapotaceae)	large tree
Erinnyis lasauxii (Bdv.)	*Sarcostemma glauca* HBK. (Asclepiadaceae)	low vine
Erinnyis oenotrus (Cram.)	*Fosteronia spicata* (Jacq.) G. Mey (Apocynaceae)	low perennial vine
Eumorpha anchemola (Gram.)	*Cissus rhombifolia* Vahl. (Vitaceae)	low perennial vine
	Cissus sicyoides L. (Vitaceae)	low perennial vine
Eumorpha satellitia (L.)	*Cissus rhombifolia* Vahl. (Vitaceae)	low perennial vine
	Cissus sicyoides L. (Vitaceae)	low perennial vine
Eupyrrhoglossum sagra (Poey)	*Chomelia spinosa* Jacq. (Rubiaceae)	sapling to treelet
	Guettarda macrosperma D. Sm. (Rubiaceae)	sappling to treelet
Isognathus rimosus (Grt.)	*Plumeria rubra* L. (Apocynaceae)	large tree
Manduca barnesi (Clark)	*Godmania aesculifolia* (HBK.) Standl. (Bignoniaceae)	sapling
Manduca corallina (Drc.)	*Cordia alliodora* (R. & P.) Oken (Boraginaceae)	sapling to large tree
Manduca dilucida (Hy. Edw.)	*Sapranthus palanga* Fries (Annonaceae)	sapling to treelet
	Annona reticulata L. (Annonaceae)	sapling to treelet
Manduca florestan (Cram.)	*Pithecoctinium crucigerum* (L.) A. Gentry (Bignoniaceae)	low perennial vine
	Cydista heterophylla Seib. (Bignoniaceae)	low perennial vine
	Tabebuia ochracea (Cham.) Standl. (Bignoniaceae)	sapling
	Callichlamys latifolia (L. Rich) K. Schum. (Bignoniaceae)	low perennial vine
	Arrabidaea chica (H. & B.) Verl. (Bignoniaceae)	low perennial vine
	Cornutia grandifolia (Schlecht. & Cham.) Schau. (Verbenaceae)	shrub
	Ceratophytum tetragonolobum (Jacq.) Sprague & Sandw.	low perennial vine

Table 3. — Continued

Larva	Host	Microhabitat
	Plenontoma variabilis (Jacq.) Miers (Bignoniaceae)	low perennial vine
	Stachytarpheta frantzii Polak (Verbenaceae)	shrub
Manduca lefeburei (Guer.)	*Casearia sylvestris* SW. (Flacourtiaceae)	sapling to treelet
	Casearia corymbosa HBK. (Flacourtiaceae)	sapling to treelet
Manduca muscosa (R. & J.)	*Verbesina gigantea* Jacq. (Compositae)	giant herb
	Lantana camara L. (Verbenaceae)	shrub
	Lasianthaea fruticosa (L.) K. Becker (Compositae)	shrub
	Baltimora recta L. (Compositae)	herb
	Melanthera aspera (Jacq.) Small (Compositae)	herb
	Wedelia calycina L. C. Rich (Compositae)	herb
Manduca occulta (R. & J.)	*Solanum ochraceo-ferrugineum* (Dun.) Fern (Solanaceae)	herb
	Solanum hazenii Britt. (Solananceae)	herb
	Solanum accrescens Standl. & Mort. (Solanaceae)	herb
	Cestrum DHJ 12029 (Solanaceae)	shrub
Manduca rustica (F.)	*Lantana camara* L. (Verbenaceae) [a]	shrub
	Stachytarpheta frantzii Polak (Verbenaceae)	shrub
	Cordia panamensis Riley (Boraginaceae)	sapling
	Pithecoctenium crucigerum (L.) A. Gentry (Bignoniaceae)	low perennial vine
	Amphilophium paniculatum (L.) HBK. (Bignoniaceae)	low perennial vine
	Merremia umbellata (L.) Hall (Convolvulaceae)	herb vine
	DHJ 12071 (Convolvulaceae)	herb vine
	Hyptis verticillata Jacq. (Labiatae)	herb
Manduca sexta (L.)	*Capsicum annum* L. (Solanaceae)	herb
	Lycopersicon esculentum MIll. (Solanaceae) [a]	herb
Neococytius cluentius (Cram.)	*Piper marginatum* Jacq. (Piperaceae)	shrub
Nyceryx coffeae (Wlk.)	*Calycophyllum candidissimum* (Vahl.) DC. (Rubiaceae)	sapling to large tree
Pachygonia drucei R. & J.	*Doliocarpus dentatus* (Aubl.) Stand. (Dilleniaceae)	low perennial vine
Pachylia ficus (L.)	*Ficus insipida* Willd. (Moraceae)	sapling to large tree
	Ficus continifolia HBK. (Moraceae)	sapling to large tree
	Ficus obtusifolia HBK. (Moraceae)	sapling to large tree
	Ficus ovalis (Liebm.) Miq. (Moraceae)	sapling to large tree
	Brosimum alicastrum Swartz. (Moraceae)	sapling

Table 3. — Continued

Larva	Host	Microhabitat
	Chlorophora tinctoria (L.) Gaud. (Moraceae)	sapling to large tree
	Castilla elastica Cerv. (Moraceae)	sapling
Pachylia syces (Hbn.)	*Ficus ovalis* (Liebm.) Miq. (Moraceae)	large tree
Pachylioides resumens (Wlk.)	*Forsteronia spicata* (Jacq.) Mull (Apocynaceae)	low perennial vine
Perigonia lusca (F.)	*Calcophyllum candidissimum* (Vahl.) DC. (Rubiaceae)	sapling to large tree
	Guettarda macrosperma D. Sm. (Rubiaceae)	sapling to treelet
Protambulyx strigilis (L.)	*Astronium graveolens* Jacq. (Anacardiaceae)	sapling to large tree
	Spondias mombin L. (Anacardiaceae)	sapling to large tree
Pseudosphinx tetrio (L.)	*Plumeria rubra* L. (Apocynaceae)	large tree
Sphinx merops Bdv.	*Lantana camara* L. (Verbenaceae) [a]	shrub
	Hyptis pectinata Poit. (Labiatae)	herb
Unzela pronoe (Drc.)	*Tetracera volubilis* L. (Dilleniaceae)	low perennial vine
Xylophanes anubus (Cram.)	*Psychotria nervosa* Sw. (Rubiaceae)	shrub
	Psychotria horizontalis Sw. (Rubiaceae)	shrub/herb
Xylophanes ceratomioides (G. & R.)	*Hamelia patens* Jacq. (Rubiaceae)	shrub
Xylophanes chiron Dry.	*Psychotria pubescens* Sw. (Rubiaceae)	shrub
	Psychotria horizontalis Sw. (Rubiaceae)	shrub
	Faramea occidentalis (L.) A. Rich. (Rubiaceae)	sapling
Xylophanes juanita R.	*Psychotria pubescens* Sw. (Rubiaceae)	shrub
	Psychotria horizontalis Sw. (Rubiaceae)	shrub/herb
	Psychotria nervosa Sw. (Rubiaceae)	shrub
Xylophanes maculator (Bdv.)	Psychotria horizontalis Sw. (Rubiaceae)	shrub/herb
Xylophanes pluto (F.)	*Hamelia patens* Jacq. (Rubiaceae)	shrub
Xylophanes porcus (Hbn.)	*Hamelia patens* Jacq. (Rubiaceae)	shrub
Xylophanes turbata (Hy. Edw.)	*Hamelia patens* Jacq. (Rubiaceae)	shrub to treelet
	Psychotria microdon (DC.) Urban (Rubiaceae)	shrub/herb
Xylophanes tyndarus (Bdv.)	*Faramea occidentalis* (L.) A. Rich. (Rubiaceae)	treelet

[a] Host plant introduced to Santa Rosa National Park.

revealing addendum to this pattern is that if those same saturniid caterpillars are placed on small saplings inside screen nets, they develop into quite normal adults. This is true whether they are transferred as first-instar or any later-instar caterpillars. I have done this with *Rothschildia lebeau* on *Spondias mombin* L. and *Xanthoxylum setulosum* P. Wilson; *R. erycina* (Shaw) on *Exostema mexicanum* A. Gray and *Coutarea hexandra* (Jacq.) Schum.; *Eacles imperialis* (Dry.) on *Cochlospermum vitifolium* (Willd.) Spreng.; *Citheronia lobesis* W. Rothschild on *Calycophyllum candidissimum* (Vahl.) DC., *Spondias mombin*, and *Cochlosperum vitifolium; Arsenura armida* (Cram.), *Caio championi* (Drc.), and *Titaea tamerlan* (Maassen) on *Bombacopsis quinatum* (Jacq.) Dugand; *Othorene purpurascens* (Schaus) on *Manilkara chicle* (Pittier) Gilly; *Othorene verana* (Schaus) on *Quercus oleoides; Syssphinx molina* (Cram.) on *Pithecellobium saman* (Jacq.) Benth., *Cassia grandis* L., and *Albizzia adinocephala* (Donn. Sm.) Britt. & Rose; *Syssphinx colla* (Dyar) on *Pithecellobium saman; Adeloneivaia isara* (Dognin) on *Lysiloma divaricata* (Jacq.) Macbride and *L. auritum* (Schl.) Benth.; and *Dirphia avia* (Stoll) and *Schausiella santarosensis* Lemaire on *Hymenaea courbaril*. The net protects the caterpillars from carnivores but does not, I assume, seriously modify the microclimate of the plant's physiology.

The opposite experiment, putting these species of saturniid larvae on a host plant sapling in nature without a protective net, results in rapid removal of the caterpillars by ants, wasps, birds, scorpions, mammals, and spiders. The few survivors are very often parasitized. I am in the process of conducting large-scale experiments which will yield an understanding of the variation and how it compares with the mean and variance of the same experiments in adult host plant crowns. However, a few preliminary results are instructive.

On 18 July 1983, I placed 340 first-instar, newly hatched *Rothschildia lebeau* caterpillars on a 4-m tall bushy *Spondias mombin* sapling growing in a tangle of secondary succession. The lower trunk was ringed with Tanglefoot, and the surrounding vegetation was trimmed so that the host plant did not contact any other plant. By 8 August, 21 days later, only 13 caterpillars remained, all late penultimate instar. On 15 August, 3–5 days before they were due to wander off the plant to pupate, I removed the 12 remaining survivors, all of which spun cocoons. Of these caterpillars, 5 contained a large ichneumonid wasp larva *(Enicospilus)*, 3 contained larvae of tachinid flies, 3 died of disease inside their cocoons before they could pupate, and 1 produced a healthy pupa.

On 30 June, I placed 120 third- and early fourth-instar larvae of *Syssphinx molina* on 60 sapling *Pithecellobium saman* growing in roadside secondary succession within 100 m of adult *P. saman*. Shortly before these larvae (Fig. 5A) were due to leave the plant to pupate in the litter and only 11 days after they had been placed out, I collected the 14 survivors. Three of these contained larvae of a species of *Thyreodon*, an ichneumonid wasp apparently specific to this caterpillar and its close relatives, and six produced healthy pupae; the remainder died of disease. As yet I have no extensive data on the survivorship of *Rothschildia lebeau* or *Syssphinx molina* caterpillars in the crowns of their large tree host plants, but numerous anecdotal observations suggest that it will be greater than the low levels of survival mentioned above.

There is a very conspicuous exception to the generality that saturniids are concentrated in the crowns of adult trees. Hemileucine saturniids, the io moth to extratropical New World readers, are found both on juveniles of their hosts and on species of plants that are normally small as adults and are therefore imbedded in low secondary succession (these caterpillars are found as well in the crowns of large trees; see Table 2). Hemileucine caterpillars (Fig. 5B, C) are the most severe urticators of

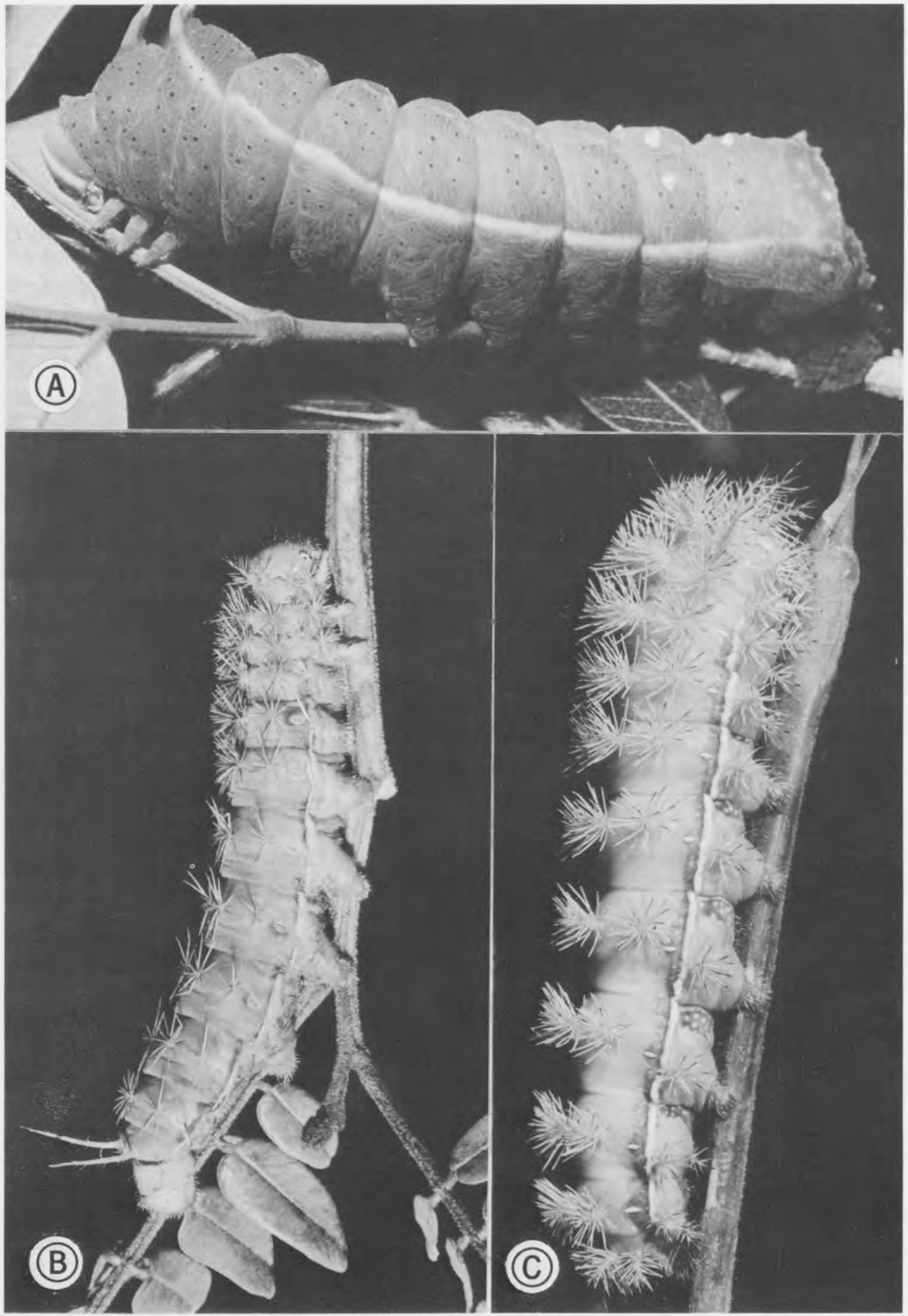

Fig. 5. — (A) Ultimate-instar larva of *Syssphinx* molina; this green morph has a greenish-white lateral stripe, yellow thoracic horns (scoli), and posterior dorsal gold toothlike spines. (B) Ultimate-instar urticating larva of *Periphoba arcaei*; this green caterpillar has a pale whitish-green lateral line with a lavender line just above it. (C) Ultimate-instar urticating larva of *Automeris io*, this green caterpillar has a white lateral line with a dark red lateral line just above it and lower lateral dark red patches with white dots. July-August 1983, Santa Rosa National Park, Costa Rica.

the saturniid world. As such they are largely invulnerable to a major subset of the vertebrate carnivores that probably find it more profitable to search for food in secondary succession than in the huge monospecific expanses of leaves in the forest canopy.

It is too early in this investigation to be able to offer a clean hypothesis about what allows sphingid caterpillars to feed on such a diversity of plant life forms (Table 3), especially on the small ones. However, some possibilities come to mind (cf. Janzen 1984b).

1. Sphingid adults live for weeks to months (as compared with 3–10 days for saturniid females) and therefore have more time to seek out widely scattered small individual hosts on which to lay only one or very few eggs at a time; with only a few nights to search for a host, a saturniid female may find it more profitable to search for a few large crowns and lay many eggs on each than to have to locate many saplings.

2. By being initially widely scattered, sphingid caterpillars avoid density-dependent effects, such as are likely to occur when, for example, a *Polistes* wasp finds one of many saturniid caterpillars on a plant and repeatedly returns to harvest them.

3. Because they are extremely host-specific, sphingid caterpillars are on average more cryptic than are saturniid caterpillars and therefore have a greater chance of surviving the visually oriented component of the more intense carnivory that, I suspect, occurs in the low vegetation of secondary succession.

4. Sphingid caterpillars grow more rapidly to a given size than do saturniids of the same body weight; they are therefore exposed to agents of larval mortality for a shorter period than are saturniid caterpillars.

5. Sphingid caterpillars may have chemical or physical defenses against invertebrate carnivores, defenses that saturniids lack. I have seen the same *Polistes* that aggressively harvests young *Caio championi* caterpillars from sapling *Bombacopsis* land on *Manduca sexta* (L.) caterpillars and simply walk on in search of food, apparently treating the caterpillars as though they were part of the plant.

Three species of "primitive" sphingids (Smerinthinae) at Santa Rosa offer instructive exceptions to the generality that sphingids and saturniids have different hosts at Santa Rosa. *Protambulyx strigilis* (L.) caterpillars are commonplace on *Spondias mombin* and *Astronium graveolens* Jacq., ranging from 1.5-m saplings to the crowns of 20-m, full-grown trees; they are found on all sizes of their hosts from forest understory to tree falls to large expanses of recent secondary succession along roads and in old fields. They are heavily parasitized by tachinids on all of these plant life forms and in all habitats. In forests, and on forest edges, *Rothschildia lebeau* (Saturniidae) caterpillars are found only in the crowns of medium-sized to large *Spondias mombin*; it is extremely difficult to imagine what besides predator pressure could have been responsible for the evolution or ecology of this restriction to adult *S. mombin*. However, since female *R. lebeau* do occasionally oviposit on sapling *S. mombin*, and I have on seven occasions found well-developed *R. lebeau* larvae on *S. mombin* saplings in secondary succession, it may be that there is little evolution involved. Rather, the *R. lebeau* females may be ovipositing throughout the *S. mombin* population, but carnivores may be eliminating those on the saplings. If this is the case, were *S. mombin* the only *R. lebeau* host plant in the park and were *S. mombin* a small treelet only found in early secondary succession, *R. lebeau* might well be absent from the park. It is also evident that *P. strigilis* is substantially more cryptic than is *R. lebeau* when on *S. mombin*.

Amplyterus gannascus (Stoll) and *A. ypsilon* R. & J., the other two smerinthine sphingids at Santa Rosa, feed exclusively on *Ocotea veraguensis*

(Meisn.) Vlez. *O. veraguensis* is a shrubby subcanopy treelet found throughout the understory of several forest types at Santa Rosa. It is the only lauraceous plant in the habitat. *A. gannascus* and *A. ypsilon* are encountered feeding on the foliage of *O. veraguensis* at all heights, from 1-m saplings to the tops of the crowns of 8-m tall large adult plants. The saturniid *Copaxa moinieri* Lemaire has *O. veraguensis* as its sole host at Santa Rosa. In contrast to other saturniids, *C. moinieri* is conspicuous in feeding entirely on the saplings and lower branches of its host and is virtualy never found more than 3 m above the ground. *O. veraguensis* may range from forest edge to heavily shaded forest understory, but the vast majority are in the forest understory. However, if the caterpillars are placed on foliage in crowns of adult *O. veraguensis* under protective nets or on similar foliage in plastic bags in the laboratory, they develop quite normally. Here again, the sphingid feeds throughout the life forms of its host plant, while the saturniid is restricted to a particular subset of its host population. While as yet untested, one selective pressure for this behavior is easy to postulate. Since the host is a forest understory plant, feeding solely on the foliage within about 3 m of the ground places caterpillars in a zone quite free of foraging by white-faced monkeys. White-faced monkeys are eager to eat large caterpillars, and in the last instars, the caterpillars of *C. moinieri* are quite easy to find because of the characteristic damage that they do when feeding. This is so when there is a defoliation event, at which time the leafless shrubs are cleaned of caterpillars by the human collector, and presumably would be as well by insectivorous monkeys if they foraged close to the ground.

There are at least six other species of *Copaxa* in Costa Rica. A summary of *Copaxa* host records (Janzen unpublished manuscript) suggests that they are specialists on Lauraceae and may be able eat the foliage of any species of *Ocotea*, *Nectandra*, or *Persea*. Why then don't they occur at Santa Rosa, where *O. veraguensis* is common? At least three species of *Copaxa* occur only 10–13 km to the east in a more evergreen forest that is continuous with the Santa Rosa forest. Could it be that these other species of *Copaxa* feed higher in the foliage of their host plant and therefore don't survive at Santa Rosa because this zone is lethal on *O. veraguensis* in the dry forest of lower stature, as found at Santa Rosa?

In short, when a sphingid hops to a new host plant, it gets more than the plant's chemistry. The plant's nutrient value may be high and its defenses may be easily bypassed by existing chemical pathways, but if a green caterpillar has to sit on a brown leaf all day, its fitness on that plant may well be zero. Likewise, if a species of saturniid caterpillar is essentially immune to most vertebrate carnivores because it has severely urticating spines, it has a major trait that predisposes it to the evolution of the biochemical ability to feed on a variety of host species. This appears to be the case with the hemileucine saturniids. They, severe urticators, are found on many kinds of leafy backgrounds, as indicated by their long host lists.

On the other hand, I do not wish to denigrate the importance of plant chemistry in all of this. If a caterpillar lineage comes up with a high quality general-purpose detoxifying system, as the ancestral species to the hemileucines must have done, then the mutant that subsequently invented urticating hairs had the companion trait necessary to allow the explosive radiation that produced and maintained the most species-rich and widespread of the four New World saturniid subfamilies. Over half the New World saturnids are hemileucines; the most species-rich genus, *Hylesia*, with over 200 species (C. Lemaire personal communication), has not only severely urticating caterpillars (see Janzen 1984a for a review), but aggregating caterpillars as well.

CAN A CATERPILLAR GET A FREE RIDE?

A major aspect of the evolutionary accumulation of a plant species' herbivore load is the intensity of fitness depression of the plant by an evolutionarily incoming caterpillar. Put most simply, the more severe is the caterpillar's impact, the more likely is the newcomer to depress the density or local distribution of the plant to a level at which it will not support the caterpillar population or will select for a defense trait that will evict a portion of the herbivore load, or both. In short, one expects that the smaller the bite the herbivore takes, the more likely it is to be able to persist on a new host plant. But bites are measured not in grams of seeds or area of leaves, but in units of population change or fitness depression.

There is, however, one rarely discussed way in which a herbivore can take large bites without depressing the fitness of the host plant. If the herbivore feeds on a subset of the host population that is fated to die prior to reproduction irrespective of the herbivore's impact, it will have no fitness-depressive effect whatsoever. Additionally, if it feeds on a plant that will live to reproduce, then the fitness-depressing effect of its herbivory should be directly proportional to the fitness of that plant relative to its conspecifics. In other words, the worst way to move evolutionarily among host species or increase your host list is to take big bites out of the individuals of the population with the highest potential fitness. At the opposite extreme are the herbivores that feed on plants that are clearly genetically dead though physiologically living – the green aborted leaf or fruit on the forest floor, the branch newly broken out of the tree crown, the seed defecated on the floor of a dry bat cave, the annual herb that has matured and shed its seeds, and so on. A detritivore is defined as an organism that feeds on a dead plant (or animal), and from the viewpoint of evolutionary ecology, *dead* is defined as having zero potential fitness. While no living wild plant has zero probability of surviving to first reproduction, it is certain that the probability of attaining any given fitness value is neither distributed evenly among the members of the population nor at random with respect to a multitude of environmental variables. The questions become whether sufficient cues exist by which herbivory can be evolutionarily or ecologically directed so that its impact is reduced, and whether individual selection can generate the necessary traits. To ask the question in a different way, are there caterpillars with little or no impact on their host populations simply because they feed (for whatever reason) on that subset of the plant population that has severely reduced potential fitness?

Such a set of questions calls attention to a major difference between plants and animals as hosts or prey. Since animals move around, it is harder to identify individuals, cohorts, or arrays that have a high likelihood of not attaining full adult status than is the case with plants. Despite the fact that we all know about this difference, ecologists have not developed either a terminology or conceptual base with which to discuss easily its potential significance to competition, herbivory, edaphic responses, etc.

Before examining some examples at Santa Rosa, a hypothetical example is in order. First, consider the case of a monophagous caterpillar species that is distributed over its host plants in a manner unrelated to the probability of any particular plant's attaining its potential fitness. Assume the caterpillar to be on 20 percent of the host individuals and that each caterpillar set (on each plant) eats half the leaves off its plant before pupating. The 10 percent of the plant population with a moderate chance of becoming adult (e.g., individuals growing in tree falls) will have 20 percent of its individuals damaged to this degree. The remaining 90 percent of the plant population will be damaged likewise, but assume that only 1 percent of these plants have a chance of surviving (i.e., those growing where a tree *will* fall). With respect to natural selection, the selective pressure for a defense trait that will repel the caterpillar is generated by 50 percent herbivory of 20 percent of 10.9 percent of the individuals, while the amount of leaf eaten by the caterpillar population is 50 percent of 20 percent of 100 percent of the individuals. In short, enough leaf material to sustain a species of caterpillar may be harvested with only the amount of impact that would have been generated by a much less voracious species of caterpillar feeding on a plant population with a high proportion of individuals with a high chance of attaining their potential fitness. Alternatively, if the incoming caterpillar fed only on individuals with a high chance of surviving, it would have the same impact with much less herbivory that it would have if it also included ill-fated conspecifics in its diet. This scenario may also be stated as, "The more the caterpillar population is focused on ill-fated plants, the more likely it is to persist." At the limit, the caterpillar feeding on shed leaves is totally free of evolutionary responses by the plant to its feeding. Likewise, as the percentage of the plant population made up of ill-fated plants rises, there is a rise in the amount of herbivore load that will be sustained free of selective charge if the herbivores are distributed at random or focused on the ill-fated plants.

Two kinds of ecological complexity should be added to this hypothesized process. First, if the herbivory raises the probability that a plant will die before reproduction or that it will be a less prolific reproducer, there is the complication that the same amount of herbivory is likely to lower the realized fitness of a weakened plant more than that of a healthy one. This differential response may alleviate some of the ill-fated plant effect (eliminate some of the free ride) by rendering the herbivore less of a detritivore and more of a predator or parasite.

Second, while the herbivore subsisting largely or totally on ill-fated plants may not be selecting for traits to repel itself even if this leads to earlier plant death than would otherwise have occurred, it will still be ecologically thinning out its host plants. Furthermore, it will have to survive despite the defenses selected for by other more fitness-reducing species of herbivores, just as must the more conventional detritivores consuming litter.

It is critical to recognize that the selective process that may result in a larger herbivore load on ill-fated individuals or in larger herbivore loads on species that normally have a high proportion of ill-fated individuals does not favor local mutant herbivores for this trait per se. The individual herbivore that feeds on an ill-fated plant in preference to a plant with high potential fitness does not raise its own fitness. Rather, the selective process is that of the plant suffering or repelling herbivores that are serendipitously arriving through the evolution of other traits or by immigration.

What fraction of the leaf-eating herbivores in Santa Rosa habitats are largely supported by ill-fated plants with little or no potential fitness? Furthermore, what proportion of the herbivores subsists on ill-fated plants because those plants were actively sought by ovipositing females or because their habitats are so sought? In both cases, I assume that the selection for this choice was not driven by a selective value to the individual female ovipositing on the plant with a low potential fitness. It is easy to imagine that many of the Santa Rosa seed predators subsist on seeds that have zero fitness because of their site of deposition following dispersal (or lack thereof). It is much more difficult to divine the potential fitness of the young growing plants whose leaves are important food for so many caterpillars at Santa Rosa. There certainly are many species of caterpillars at Santa Rosa that wholly or largely feed on saplings of forest canopy trees in the deeply shaded understory where the host has virtually no chance of survival to reproduction unless a tree fall occurs at that site. I cannot yet offer data on the influence of this herbivory on how long a plant can wait before finally dying of starvation, distorted stems, disease, etc.

CLIMATE IS A HOST-PLANT TRAIT

The physical environment undoubtedly influences caterpillar fitness. We tend to forget that each local population of plants, and even distinctive subsets of the population, is associated with a distinctive microclimate. The caterpillar has to contend with this as much as with the directly genetically programmed traits of the plant and the plant's distinctive carnivory regime. Variation in this climatic regime over a plant's distribution may as well as responsible for the absence of a caterpillar in parts of the plant's range as is geographic variation in host plant chemistry. That the saturniid moth *Schausiella santarosensis* is apparently found only in northwestern Guanacaste Province, Costa Rica, while its host tree, *Hymenaea courbaril*, ranges from southern Mexico to central South America, could have many causes besides local uniqueness of *H. courbaril* chemistry. Among these causes may be the Santa Rosa climate.

At Santa Rosa, there are many examples of climatic components of what might be termed the suitability profile of caterpillar host plants. One that is annoyingly omnipresent is the failure of many species of saturniids to have at least the minimum of three generations per year that could occur if host foliage properties were the only challenge to the caterpillar. While in theory such failures may be equally attributable to seasonal change in carnivory risk or leaf chemistry, there are times when climate seems to be the likely primary cause.

The four saturniids that feed on the foliage of *H. courbaril* offer an example. This tree bears resin-rich leaves (e.g., Langenheim et al. 1982) throughout the year, except for approximately 2 weeks in December or January (early dry season) when the old leaf crop is dropped and a new one is put out immediately thereafter. All four species of saturniids that eat *H. courbaril* leaves can be reared readily under nets in the field or in plastic bags in the laboratory on foliage collected at any time of year (unpublished field notes).

H. courbaril foliage of all ages is eaten by all four species in nature and in the laboratory. Throughout the dry season, from at least January until shortly before the first rains in late April or early May, three of the four saturniids are dormant in cocoons or as pupae in the litter below the fully leafed adult *H. courbaril*, and *Hylesia lineata* Drc. is dormant as eggs in an arboreal felt nest constructed by the female (Janzen 1984a). *Dirphia avia* anticipates the rains and times its emergence so that ovipositing females are in the forest as much as a week before the rains. The eggs require 2–3 weeks to hatch, with the consequence that the caterpillars begin feeding during the rains. *Schausiella santarosensis, Periphoba arcaei* (Drc.), and *Automeris zugana* Drc. adults emerge within 3 weeks after the first heavy rains, and their first-generation caterpillars are present for the first 2–3 months after the rains begin. *H. lineata* eggs hatch shortly after the rains begin as well, with the same consequence. Most of the pupae of the first generation of *S. santarosensis* remain dormant in the variably wet and dry litter below the *H. courbaril* for 9–10 months before eclosing to repeat the process the next year; however, a small fraction of these pupae eclose about 3 weeks after pupation and constitute a second generation during the second half of the rainy season. This latter generation again demonstrates that the leaves of *H. courbaril* are chemically quite suitable as food for *S. santarosensis* at this time of year. The pupae of this second generation then join those of the first generation in remaining dormant below the leafy trees throughout the dry season. The other three saturniids regularly have two generations on the rainy season *H. courbaril* leaf crop (as well as on other species of hosts) and then become dormant at the end of the rainy season. It is hard to avoid the working hypothesis that the reason that these moths ignore a food source on which they could pass at least two more generations is because the dry season heat and wind, and attendant desiccation, are inimical to their development in the crown of a large tree. The first-instar larvae are probably the most susceptible, but desiccation during molting and even during pupal formation may also be a problem.

Larval mortality from desiccation will probably turn out to be a major reason for delaying oviposition until the rains start, even when the host plant is in full leaf. For example, at the beginning of the 1983 rainy season (late May), there was sufficient rain to cause some *Cochlospermum vitifolium* to leaf out. This plant is a natural host of *Eacles imperialis* (Table 2). I placed hundreds of 1-day-old first-instar *E. imperialis* larvae on these leafy *C. vitifolium*. The plants were then naturally subject to winds, high temperatures, direct insolation, and dry air as severe as was characteristic of midday a few weeks earlier during the dry season. It was dry enough to stop further *Cochlospermum* branch elongation. While the caterpillars did feed, few obtained enough water to replace that lost by desiccation, and I watched them quite literally dry up and blow off during the following 2 days. Two weeks later, after rainy season humidity, cloudiness, and still air had set in, similar inoculations of the same plants resulted in nearly 100-percent larval survival (the larvae were protected from carnivores with netting in these experiments). The same change occurred with *Rothschildia lebeau* first-instar larvae put on insolated sapling *Spondias mombin* during the same days. For both species, the foliage of their host plants during the dry weather was excellent fodder when given to siblings of the dead caterpillars in plastic bags in the laboratory.

In short, at the beginning of the rather erratic 1983 rainy season, the leaves of major host plants of *E. imperialis* and *R. lebeau* were present and edible but, in effect, unavailable. In addition, there was spatial heterogeneity to their availability. Inoculation experiments, using siblings of the victims at the beginning of the rainy season, were quite successful when the young caterpillars were placed on host plants that happened to be growing in the shade and wind-buffered air of a patch of evergreen trees. Had these shaded plants been of a different species, one of the other host species of these two moths, it would be easy to conclude that these ecologically available species of host plants had different weather regimes from those of *C. vitifolium* and *S. mombin*, thereby giving them a longer period of susceptibility to the caterpillars during the year. It is likewise easy to imagine that this different regime might well make them an acceptable host for a species of caterpillar that has no other species of host in the habitat.

The weather becomes a trait of the host plant in more ways than just its direct effect on the caterpillar. By determining the duration of leafiness, the weather determines such things as the number of caterpillar generations possible. This may in turn determine the length of a generation, because the number of generations per rainy season must be an integral number. The length of a generation may in turn determine which hosts are too good and which are inadequate. An inadequate host may be one that the caterpillar can eat with impunity, yet lacks sufficient nutrients for the caterpillar to attain a reasonable size by the time it must pupate if it is to remain in synchrony with the remainder of its population. A too-good host might be one that makes the caterpillar grow too fast; however, in this case, I would expect quick selection for a fixed larval period coupled with heavier caterpillars on better host species or individuals. Viewed the other way around, a given nutrient and defensive chemistry may generate a moth egg-to-adult cycle that is incompatible with the seasonality of the site even if the resultant adult moths are quite normal in weight and other physiological paramenters.

DISCUSSION

A host plant is not the focus of the ecological and selective regime of a moth and its caterpillars. Rather, the focus is a space bounded by parameters involving carnivores, climate, host chemistry, host fitness depression through herbivory, and a variety of other traits. In a certain sense I am defining a Hutchinsonian niche for a caterpillar and arguing that this niche is not centered on any one of these traits. This notion is emphasized by recognizing that in any particular point in season, space, or ontogeny there are many individuals of the caterpillar's host plant population that are not being fed on by that species of caterpillar; this distribution is not necessarily generated by randomly placed misses, but because of predictable caterpillar failure or disinterest under this or that circumstance. A particular host is necessary, but not sufficient, for caterpillar presence.

But is it even necessary? Why not eat just any plant? The current answer, and I am sure the largely correct one, is that in any given snapshot in evolutionary time, a caterpillar species is genetically (and subsequently, ecologically as well) programmed so that it feeds on only a few species of plants in the habitat; female oviposition behavior is here viewed as merely an extension of caterpillar behavior. However, there are at least two ways in which this answer is probably incomplete. First, and I think this is generally accepted by students of animal-plant interactions, there are probably more species of plants in the habitat that can be physiologically processed by the caterpillar species than the caterpillar species actually eats in nature. I have discussed here some of the reasons why these plants may not be used as hosts; the physical climate, predators, etc., may stop the evolution of the choice of that plant, and current ecological processes may prevent its use even if it is chosen by the ovipositing female. Second, given the right collection of ecological circumstances, perhaps just about any plant would be a suitable host in ecological time and certainly in evolutionary time.

In other words, is it unthinkable that, if a species of moth were confronted with a habitat rich in plant species but quite lacking in carnivores (including diseases), inclement weather, competitors, and the ability of plants to evolve further, it might well evolve a digestive physiology such that any individual caterpillar could feed on many or even all plant species? We can imagine that the genetic programming might be too complex and that the biochemical machinery somewhat incompatible for a caterpillar to contain all the collective food-processing abilities of the several thousand species of caterpillars now feeding on the plants of Santa Rosa. But what if, instead, the caterpillar simply developed a series of biochemical filters that, albeit slowly and incompletely, simply extracted the easily removed nutrients from the food and passed the rest on out? At Santa Rosa, *Hypercompe icasia* Cram. (Arctiidae) has over 60 species of broadleafed host plants recorded for it to date (in half as many plant families) and is one of the most slow-growing caterpillars I have ever reared. The sympatric *H. suffusa* Schaus has more than 50 recorded hosts, and there is almost no overlap of its host list with that of *H. icasia*; it not only grows very slowly, but if the food dries up, it spins a flimsy silk nest and waits until more green leaves appear. It can wait as long as 3 months at ambient temperatures. Why do most other Santa Rosa caterpillars appear to lack such digestive abilities? I doubt that it is because *Hypercompe* has invented some miraculous digestive system never hit upon by other Lepidoptera. I view *Hypercompe* not as the epitome of anything, but simply one of many ways to cope with the wide variety of selective and ecological pressures that confront a caterpillar.

I have mentioned quite enough complications in this essay that it seems truly a miracle for there to be any patterns at all. However, patterns do exist. The large moths at Santa Rosa – saturniids and sphingids – can be partitioned with respect to many of the traits mentioned here. I have already mentioned that sphingids are generally found in carnivore-rich mixes of small plants in low vegetation as well as in the crowns of large trees, while saturniids are much more caterpillars of the crowns of large trees. Sphingids rely heavily on crypsis specific to the host plant (or even leave the host plant during the day), while saturniids have both ostentatious real defenses and mimicry in addition to a more generalized crypsis. Closely linked to this contrast, sphingid caterpillars are more host-specific than are saturniids and grow faster than do saturniids.

On the one hand, it is nothing new to stress that a host plant is more than just its chemistry. But the topic needs stress now for two reasons. First, most analyses of nonchemical traits (e.g., plant apparency, size of the plant, or plant population as an island) have examined them as large-scale attributes, with the stress being on how these traits correlate with some caricature of host plant chemistry or numbers of insect species (e.g., Southwood et al. 1982). Such analyses are an essential part of the story but bypass the fine-scale interactions between species and individuals (e.g., Karban and Ricklefs 1983; Lawton 1982; Rausher and Papaj 1983; Connor et al. 1983) and the small-scale nonchemical traits. The nonchemical traits deserve the same detailed attention as specificity determinants that secondary compound chemistry is now receiving. Second, the topic needs stress because of the inherent difficulty in the technology of the subject. One cannot determine a caterpillar's risk of being eaten, for example, from any intrinsic trait of the plant (or the caterpillar) that can be obtained from laboratory analyses of collected materials. Equally, the depression of host plant fitness by a caterpillar population cannot be determined from any compilation of facts about plant species, including vegetation analyses, percentage of herbivory, percentage of cover, and all those other things traditionally measured. These traits are situation dependent. They have meaning only in context.

Here it is appropriate to digress on the subject of the concept of average or baseline herbivory. Plants live a long time. Grant proposals are for 3 or fewer years, and field studies are rarely more than one to two times this duration. A commonplace herbivory regime is small amounts for a run of years, with severe defoliation occurring at long and irregular intervals. Since severe defoliation events are sufficiently far apart that any one study usually sees none or only one of them, there is a strong temptation to view them as "unusual" and therefore not to be considered in determining the intensity of herbivory. While it does not make biological sense to *average* the years of peak herbivory with the many more years of much lower herbivory, somehow the impact of the plant's lifelong herbivory regime needs to be taken to be the same norm.

In characterizing the entire herbivory regime with its causes for variation, one finds that many of the nonchemical traits of the plant take on great importance. Leaving aside herbivore-induced changes in chemistry (e.g., Edwards & Wratten 1983), the defense chemistry and nutrients in a particular set of leaves are relatively invariant as causes of herbivory fluctuation when compared with other traits. Most of the individual caterpillars that actually attempt to feed on a given species of plant either can or cannot do it. And if they can, they can do it over much or all of a plant's lifespan. It is easy to forget that much of a plant's herbivore defenses are against those animals that, because of these defenses, are virtually never responsible for any leaf loss. We are in the silly situation that much of the study of secondary compound chemical ecology occurs in the vacuum of having no idea what herbivores selected for the defenses, and the intensity of much of the herbivory we measure is determined and patterned by events generally not measured by ecologists that study herbivory. The ultimate irony is that just as in the defense budgets of nations, the largest cost levied by herbivores is probably the cost of the defenses rather than the amount of material removed during herbivory (Janzen 1983b).

I have argued that a multispecies mix of small plants has a very different carnivory regime than does an equal-sized large tree crown, which is essentially a monospecific stand. For almost all biologists, the closest approximation of the multispecies mix of small plants is roadside and old field secondary succession. Such habitats are often analogized with natural disturbance sites such as tree falls, river banks, landslides, etc. I would only emphasize that the analogy is not a close one and likely to be particularly deceptive with respect to the case at hand. For example, the old field does not have nearby intact forest as an herbivore reservoir, refuge, and barrier between small portions of the old field. Likewise, tropical roadsides are, for example, generally continually bathed in dust, which is one of the best contact pesticides known (especially for small insects like parasitoids). For example, the only reason that the *Syssphinx molina* experiments mentioned earlier could be conducted was that they were conducted along a rarely traveled paved road with no shoulders.

It is clear that any herbivore entering a new habitat is stepping into a battlefield rich in plant defenses selected for by other herbivores and by the constraints of defense economics. This situation applies even more to the nonchemical traits of a host plant, the traits I have been discussing; many of the traits of importance were not even selected for by biotic agents, to say nothing of herbivores. The opportunities for coevolution have been minimal. The traits that render a *Hymenaea courbaril* crown a low-yield area for a carnivore were certainly not selected for by the four saturniid caterpillars that feed with relative impunity on the leaves in large *H. courbaril* crowns. It is unlikely that host leaf colors, shapes, and sizes, are selected for through their rendering caterpillars of a particular species easily found by carnivores.

Unfortunately for evolutionary ecology, it is at least theoretically possible for natural processes to produce a habitat full of interacting caterpillars and their hosts with no coevolution and even very little (if any) evolution. This is particularly true for the nonchemical traits of plants. One can imagine an arriving caterpillar finding a number of edible species of plants but ending up using only a small fraction of the species and biomass because of the negative effects of processes like those mentioned in this essay. Whether the caterpillar persists until it is evolutionarily modified by the many new selective pressures put upon it should depend largely upon nonchemical factors, if there is even one species of plant present that the caterpillar can eat.

The immigration placement of a caterpillar in a new habitat, and its ecological adjustment to the plants there, has much in common with the process of the introduction of new pollinators, new dispersal agents, animal-dispersed plants, etc. At first, the persistence of the invader (or a resident newly deprived of its interactant) depends on other organisms with traits similar to those of the organisms it left behind, even if the invader cannot achieve the same level of fitness that it had originally. At least theoretically, the interactions could then continue indefinitely with no evolution – though the population structure of the incoming species might be quite different than it was where it came from (as might also be those of its new associates). In fact, it is easy to imagine a species being passed from interactant to interactant over long evolutionary time, with a truly new phenotype appearing only rarely but with largely the same phenotypes of organisms continuing to interact in this or that habitat (e.g., Janzen 1983c). Perhaps evolutionary rates proceed most rapidly where species richness is lowest, since in such a situation the probability that alternate or substitute interactants are present is lowest. Yet, there has to be enough diversity of substrate for the immigrant at least to get established. At the other extreme, if there are many similar species in a habitat, the addition of one more may result in virtually no discernible evolutionary change, because each of the ecologically similar species adjusts just a small amount.

SUMMARY

To the herbivore evolutionarily moving onto a host, or surviving there, a host plant has, in addition to its chemistry and other personal traits, a carnivore regime, weather regime, and fitness regime that must be overcome by the herbivore. The interplant heterogeneity of a Costa Rican defoliation of *Randia* treelets by *Aellopos titan* sphingid caterpillars is described as due to heterogeneity in the carnivory regime rather than in the interplant chemistry. That Costa Rican saturniid caterpillars feed primarily in the crowns of large trees while in the same habitat sphingid caterpillars are distributed over many more plant life forms and sizes is attributed to saturniids (except the severely urticating species) being comparatively incompetent at contending with the more intense carnivory regime of dense, low, and plant-species-rich vegetation rather than to saplings having different foliar chemistry than have their large parents. The saturniid phenology of there not being caterpillars on evergreen trees during the dry season in the same forest is ascribed to desiccation during this time of year rather than to different leaf chemistry in the dry season. Finally, I argue that the impact of herbivory, and hence the likelihood that it will select for defense traits against a herbivore, is related to the potential fitness of the actual plants fed upon. A plant that is slated

to die for other reasons is evolutionarily dead even if physiologically living; the accumulation, over evolutionary time, of an herbivore load by ecologically distinctive conspecifics of different potential fitness should differ with that potential fitness. Furthermore, the accumulation of an herbivore load by a species of plant may well be influenced by the proportion of the population of growing juveniles that are in the category of "evolutionarily dead."

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