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## Caterpillar Seasonality in a Costa Rican Dry Forest

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### Introduction

Caterpillars—taken here to mean the larvae of Lepidoptera—are not uniformly or randomly present in species or abundance in tropical lowland habitats. Instead, it is evident to any field naturalist that tropical caterpillar species and biomass are frequently correlated with seasonal phenomena, either directly or through their relationships with other organisms displaying seasonality. Indeed, other tropical insects are highly seasonal (e.g., Wolda 1988; Tauber et al. 1986; Nummelin 1989; Janzen 1973, 1983a,b, 1987a,c; Tanaka et al. 1987; Paarman and Stork 1987; Winston 1980) and there is no reason to expect caterpillars to be any different.

Caterpillar seasonality is particularly evident in tropical dry forest. This vegetation type once covered at least half of the terrestrial tropics (e.g., Murphy and Lugo 1986). However, it has been largely altered or replaced by agriculture, forestry, and animal husbandry (e.g., Uhl and Buschbacher 1985; Janzen 1988a,b). Ironically, the tropical dry forest caterpillar fauna is not of recent interest because portions of it are in danger of extinction (which it is), but rather because as tropical dryland agroforestry ecosystems begin to reacquire diverse cropping systems and even regenerate wildland vegetation, the caterpillar fauna becomes conspicuous as pests, hosts for parasitoids, food for valued vertebrates, and even as a source of genetic and chemical biodiversity for commercial exploitation.

A literature review of all the ways that tropical dry forest caterpillars have been associated with seasonal data or processes (e.g., Odendaal 1990; Jones 1987; Chippendale and Mahmalji 1987) would be a rewarding exercise, but it is not the intent of this chapter. Instead, my goal is to discuss descriptively a few aspects of the seasonality of a particular tropical dry forest caterpillar fauna, that of the

eastern end of Santa Rosa National Park in the Guanacaste Conservation Area in northwestern Costa Rica (Janzen 1988b). I pass up a literature review because the act of studying this caterpillar fauna, and taking the steps necessary to ensure its long-term survival (Allen 1988; Janzen 1988b,c, 1989a, 1991, 1992a; Janzen and Hallwachs 1992b; Tanglely 1990), has proven to be incompatible with the time investment necessary for a literature review. However, I do know that there is no published study or set of studies of a tropical caterpillar fauna with which the Santa Rosa caterpillar fauna can be contrasted. I justify a personal focus on the biology of *this* site by noting that it is large, complex, and probably representative of what once covered much of the neotropical dry forest, that its caterpillar fauna is taxonomically better known than is that of any other tropical wildland site, and that I am quite familiar with it.

I attempt to portray some of the seasonality of the Santa Rosa caterpillar fauna through generalizations as it appears to me at this time, sprinkled with illustrative examples. There are lifetimes of work ahead to put means and variances on these and other generalizations, and test the hypotheses advanced. I obviously do not have the time to examine more than a few examples in detail. However, there is an intensive effort to develop the Guanacaste Conservation Area (as with the other seven Areas de Conservación) as a huge biological station conserved into perpetuity (Janzen 1991; Janzen and Hallwachs 1992b), and to institutionalize the conservation of Costa Rica's biodiversity through nondestructive use under the auspices of the Instituto Nacional de Biodiversidad or INBio (Tanglely 1990; Janzen 1991). This act should create a climate for later and less rushed study of the ACG caterpillar fauna into perpetuity, along with a host of other studies.

The salient seasonal feature of the Santa Rosa dry forest caterpillar fauna is that it fluctuates enormously in biomass and proportional species composition within the year. While this general pattern is repeated annually, its intensity is highly variable, owing to both biological and climate variation.

## **Materials and Methods**

### *References*

Much of what I report here about the caterpillars of Santa Rosa's dry forest has not been published before. Rather than repeatedly state "Janzen, unpublished field notes," I adopt the convention of viewing the entire chapter as previously unpublished field notes and commentary, unless otherwise stated.

### *Study Site*

The study site is the general region of the administration area in the southeastern end of Santa Rosa National Park (Parque Nacional Santa Rosa) in the Guanacaste



in a patch of approximately 60,000 ha of dry forest remnants extending from the Pacific Ocean to the western foothills of the Cordillera Guanacaste (Volcan Orosí, Volcan Cacao, Volcan Rincon de la Vieja). In these foothills, the dry forest blurs into the wetter rainforests that extend then eastward to the Caribbean.

Virtually all the ACG dry forest has been cut, cleared, selectively logged, pastured, and/or farmed one or more times by European-style agrobusiness during the past four centuries. Prior to this it was occupied by indigenous peoples for at least 10,000 years (see Janzen and Martin 1982). It thus comprises an extremely complex mosaic of secondary succession ranging from 1 to 400-plus years in age. Dotted through this mosaic are a few small patches of forest with a structure similar to that of the original forest. Despite this extensive disturbance, there is no hint of the recent extinction of any dry forest species of animal or plant from the ACG other than the scarlet macaw (*Ara macaw*) and the extinctions associated with the Pleistocene megafaunal extinctions (see Janzen and Martin 1982).

However, the relative densities of the animals and plants in the ACG dry forest—and thus the qualitative and quantitative traits of many of their interactions—are (at present) clearly not those that would occur in this site were it never to have been touched by indigenous and European societies after the Pleistocene extinctions. This ecological situation applies to all neotropical dry forest north of the Panama canal. Of the interactions reported here, all are to some degree modifications of what they would be in a pristine world. However, the more the interaction depends on direct genetic traits, the less the modification. For example, whether a species of caterpillar snips or chews leaves (Bernays and Janzen 1988) is quite unaffected by whether the caterpillar is feeding early or late in the rainy season, but the relative abundance of caterpillars using these two different ways to process leaves varies strongly with the seasonal cycle.

The geology, general history, general biology, etc. of the site has been discussed elsewhere (e.g., Janzen 1986a,c,b, 1987b–g, 1989b). Below, I focus briefly on site characteristics that are direct concern to caterpillar seasonal biology.

### *Vegetation Type*

The eastern Santa Rosa forests have been described as dry forest (Holdridge et al. 1971), deciduous and semideciduous forest (Gomez 1986), etc. Rather than descend into a vegetation nomenclature of doubtful biological significance, suffice to say that the vegetation of the study site is that which is generally termed tropical dry forest, seasonal forest, deciduous forest, semideciduous forest, wet–dry forest, and/or monsoon forest (Ridpath and Corbett 1985).

The eastern Santa Rosa forests are highly variable from hectare to hectare in stature, appearance, deciduousness, and species composition (e.g., Janzen 1988b). There are three primary climatic sources of this variation, all relating to seasonality. First, small differences in exposure, drainage, and soil depth result

in strong differences in availability of water to plants of different sizes and demands. This in turn results in striking differences in plant species composition, within species deciduousness, stature, growth rate, etc. Since the flora is a mix of evergreen and deciduous species, and since many of the deciduous species vary the duration and intensity of deciduousness with the amount of water that they get, the result is a fine-scale patchwork of degree of deciduousness. This in turn creates a fine-scale patchwork of understory moisture levels, shade, temperature levels, etc. Second, the amount and pattern of rain vary strongly from year to year, again directly influencing the pattern of deciduousness through the process just described. Third, when a forest with a given degree of deciduousness is cleared or otherwise severely perturbed, for centuries afterward the subsequent successional stages are much more deciduous than was the "parent" forest. In general, the Santa Rosa dry forests of today are substantially drier than were the same forests just a few centuries earlier, simply because they are successional.

The Santa Rosa dry forests are distinctly different from Costa Rican lowland rain forest on well-drained soil. The dry forests have

- only about 20–40% of the number of plant species per large area (the study site contains only about 600 species of angiosperms, Janzen and Liesner 1980, while an area of Costa Rican lowland rain forest of comparable habitat complexity contains more than 2000 species.
- a lower canopy (5–40 m in height),
- relatively few epiphytes (but are rich in vine biomass and species), and
- several dozen very common species of trees, shrubs, and large woody vines (among which are scattered hundreds of other species).

By way of contrast, Santa Rosa animal faunas are nearly as species-rich as are those of nearby rain forest, except for amphibians and other taxa that require nearly year-round moisture. This dry-wet equivalence appears to be largely because Santa Rosa's vegetation supports both a distinctive dry forest fauna and large numbers of what are thought of as rain forest species (e.g., Janzen 1986a). Likewise, for many major taxa the Santa Rosa biomass of active animals certainly exceeds that of nearby rain forest areas during the first 2–12 months of the rainy season, but active animal biomass during the dry season is substantially lower than that of rain forest throughout the year.

#### *Climate and Weather.*

For about 6 months of each year the Santa Rosa dry forest is sunny, hot, and dry. It is extremely windy (from the northeast) during the first 3 months of the dry season (late December through mid-March). There are reliable rainfall and temperature records from the Santa Rosa weather station in the park administration area that extend from July 1979 to the present. From 1980 to 1989, the average



Figure 14.2. The total annual rainfall at the Weather Station in southeastern Parque Nacional Santa Rosa, Area de Conservación Guanacaste, northwestern Costa Rica.

rainfall was 1614 mm per year (Santa Rosa National Park weather station records). The variation in total rainfall ranges from 915 to 2558 mm per year (Fig. 14.2). While such variation in total rainfall is of extreme importance to agriculture and pasture industries, it often seems to be of less importance to the caterpillars and their interactants than is the detailed distribution of the rain within the year. A year that is too dry for an unirrigated dry-land rice crop in Guanacaste Province, for example, may receive quite enough rain for a normal crop of forest caterpillars, especially if that low rainfall is uniformly distributed during the first half of the rainy season and continues to appear after the first rainstorm.

There is an obvious within-year rainfall pattern (Figs. 14.3, 14.4) that is repeated annually. After approximately 6 months with no rainfall, the rains begin sometime between late April and mid-May. They peak during a 1- to 2-month period and then decline during the short dry season ("veranillo"). During September–November the rains intensify again. The long dry season is substantially hotter than is the rainy season (Figs. 14.3, 14.4). During the first half of the long dry season, mild to gale-force winds blow from the northeast; these are strongest during the day and the first half of the night.

There is extreme interyear variation in the stopping and starting dates of the rainy season(s) (e.g., compare Figs. 14.3 and 14.4), the duration of the windy period, the weekly temperatures of the wet or dry season, the continuity of the rainy season once started, the total amount of water to fall during the rainy season, etc. All of these kinds of variation have a conspicuous but complex impact on the caterpillar biomass and species composition in the eastern Santa Rosa dry forest.



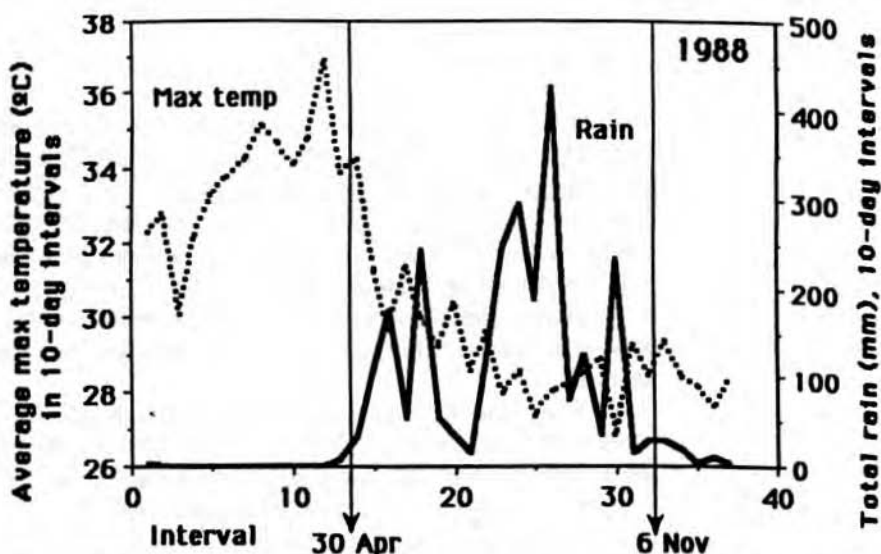


Figure 14.3. Total rainfall during 10-day intervals and the average maximum temperature over 10-day intervals in 1988 at the Weather Station in southeastern Parque Nacional Santa Rosa, Area de Conservación Guanacaste, northwestern Costa Rica.

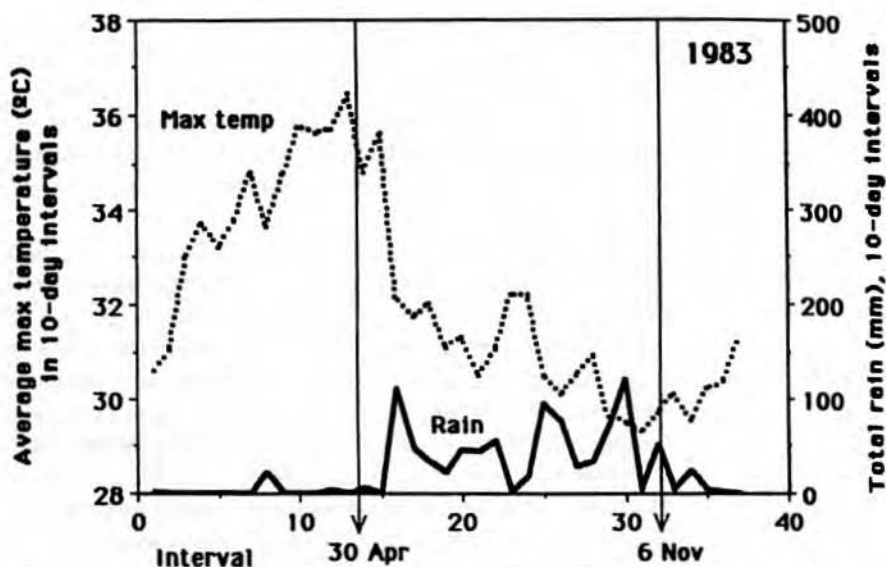


Figure 14.4. Total rainfall during 10-day intervals and the average maximum temperature over 10-day intervals in 1983 at the Weather Station in southeastern Parque Nacional Santa Rosa, Area de Conservación Guanacaste, northwestern Costa Rica.

### *Caterpillar Fauna.*

The 600 species of angiosperms in the study site support about 3140 species of caterpillars (Janzen 1988d). This is twice the number to be found in a similar large area around Ithaca, New York (42° N lat.), and roughly 12 times the number to be found in a similar area around Kevo, northern Finland (70° N lat.) (Janzen 1988d). The Santa Rosa caterpillar fauna is about 37% external plant feeders, with the remainder living in leaf rolls or mines in leaves, stems, seeds, fruits (e.g., Janzen 1983a), flowers, and roots. A very few species live in mammal nests (e.g., Davis et al. 1986), wasp nests, dung accumulations, and other bizarre habitats.

All Santa Rosa Papilionidae, Pieridae, and Nymphalidae have names and are easily identified (DeVries 1987). Probably all the other butterflies also have names, though many species remain to be collected. At least 90% of the Santa Rosa macromoth and Pyraustinae (Crambidae) have been described. The microlepidoptera are less well known taxonomically, but many of them have also been described. Most of the Santa Rosa Lepidoptera names were applied well before 1977 (see Fig. 14.6), the date of the beginning of this study. The healthy taxonomic situation with the Santa Rosa caterpillar fauna is due to most Santa Rosa Lepidoptera (as with other organisms) having ranges that extend across many degrees of latitude and countries. Santa Rosa species were described from the United States, Venezuela, Brazil, Mexico, Guatemala, etc. Lest this situation be thought to be unusual, I should point out that it also applies to macrolepidoptera faunas in most other parts of Costa Rica (and the neotropics). The problem that ecologists have with achieving taxonomic certainty with neotropical butterflies and macromoths is generally not due to a lack of species descriptions per se, but rather a lack of geographic or large-taxon revisions and/or field guides and curated reference collections.

Association of caterpillars with described adults is at a far more primitive state. The effort to rear all Santa Rosa species of caterpillars, and thus associate them with an adult and at least one wild host plant, began in 1977 and has not been repeated elsewhere in the neotropics. By September 1990, 341 species of Santa Rosa macromoths (and 116 butterflies) have been reared and are identified or have their identification in process. All Santa Rosa saturniid larvae and nearly all sphingid larvae are known (e.g., Janzen 1982, 1984a, 1985a).

Perhaps the most conspicuous feature of the Santa Rosa caterpillar fauna is its extreme abundance and omnipresence during the first 3 months of the rainy season (May–July), the large number of quite conspicuous species, the large number of carnivores (species and biomass) that feed on caterpillars during the first 3 months of the rainy season, and the massive amounts of leaf consumption at this time. It is much easier to find caterpillars in the Santa Rosa forest during these 3 months than in any Costa Rican rain forest.

During the second half of the rainy season, the caterpillar fauna is substantially



reduced (e.g., Janzen 1980a) but it is still easier to locate caterpillars than it is in rain forest at any time of year. During the dry season, caterpillars are almost nonexistent except for miners in a variety of substrates and (in a few cases) prepupae in cocoons or underground chambers. The most conspicuous feature of the Santa Rosa caterpillar fauna over successive years is how greatly it changes in biomass from year to year, and that different hosts are heavily fed on in different years (e.g., Janzen 1981). For example, in the past 12 years, no species of plant has been heavily defoliated in more than one year, and in 1977 (Janzen 1980a) there was easily 10 times as much biomass of caterpillars as has been seen in any one of the following 13 years. However, these interyear variations in caterpillars are not the subject of this chapter.

### What Really Happens When the Rains Begin?

#### *Cueing*

There is a strong temptation to view the seemingly abrupt appearance of moths, butterflies, and caterpillars at the beginning of the Santa Rosa rainy season as "cued by the rain." Those of us from northern latitudes tend to imagine that multitudes of dormant pupae have been wetted by the rains, and then eclosed to produce the egg-laying females. Such cueing does not appear to be the case.

As is clear in Figures 14.3 and 14.4, the first rains occur at the end of the hottest time of the year and are associated with an abrupt drop in the daytime average maximum temperatures. The first days following the arrival of the rains can be as much as 6°C cooler than they were a week before during the dry season. All indications are that it is the drop in temperature that the dormant pupae, inactive adults, and/or incoming migrants are using as their cue.

The eclosion times of an experimental cohort of *Rothschildia lebeau* (Saturniidae) illustrates this. In the end of the 1982 rainy season, 416 sibs of *R. lebeau* (voucher number 83-SRNP-1500) were reared to cocoons (Janzen 1984b). Almost all of the pupae became dormant (probably in response to the warming weather in December). Their cocoons were hung in airtight plastic bags in the ceiling of an outdoor laboratory at Santa Rosa, a laboratory through which there is open air circulation. Each cocoon was in a separate bag. Half of the cocoons were in air-dry bags, and the other half were maintained at 100% relative humidity by soaking a mat of wet toilet tissue in the bottom of the bag every 3–5 days. Figure 14.5 shows the eclosion pattern of the 175 females in relation to the temperature drop at the onset of the rainy season in 1983. They obviously did not eclose in response to the rain per se, since the rain never went near the bags and the dry bag cocoons were dry at the time of eclosion. Being wet or dry did not affect the pupal eclosion times at the scale of resolution displayed in Figure 14.5 (though in fact the moths in wet bags had an average eclosion date 1–2 days later than did those in dry bags).

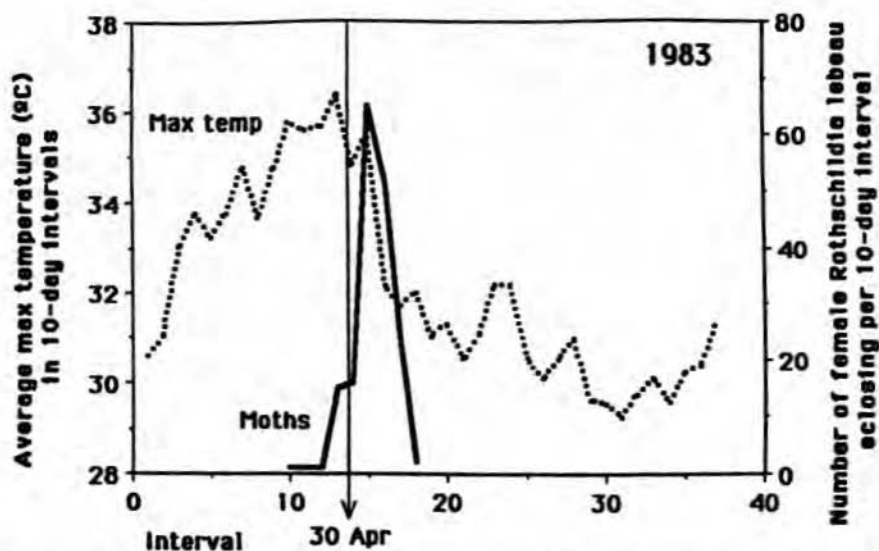


Figure 14.5. The average maximum temperature over 10-day intervals in 1983 and the dates of eclosion of a cohort of 175 sib *Rothschildia lebeau* (Saturniidae) females, summed over 10-day intervals in 1983 (see text).

A *R. lebeau* female mates on the night of eclosion and lays about half of her eggs the following night. The eggs take 6 days to hatch. The pupal eclosion dates (Fig. 14.5) plus 7 days are therefore an exact chronology of the dates of appearance of the first instar larvae in nature (wild-caught females at lights mapped exactly onto the eclosion distribution in Fig. 14.5). However, it is clear from the phenology of this cohort of sibs that the timing with the onset of the rains is not perfect (compare Fig. 14.4 and Fig. 14.5). More than 2 months of variation in the eclosion time from a single cohort (10 April to 24 June in this case) creates substantially overlapping generations during the remainder of the rainy season.

Dependence on a temperature cue is also suggested by univoltine species that normally remain dormant from the end of their annual larval stage (late June to early July) until the beginning of the next rainy season, 10–11 months later. In 1987 the short dry season (July–August) was exceptionally hot and dry. By early July, I had numerous pupae of *Manduca dilucida*, a locally common dry forest univoltine sphingid, hanging in dry plastic bags in the ceiling of the Santa Rosa laboratory “in storage” for use in the following year. However, when the rains began in September, and the temperature simultaneously dropped, about 18% of these moths eclosed within 2 weeks, despite the fact that their bags were full of dry air. Those that did not eclose then remained dormant until the following May (in synchrony with the free-living population). It seems extremely likely that eclosion of *M. dilucida* requires first a long hot period, followed by an abrupt

transition to a cooler regime. Normally, this occurs in the annual seasonal cycle, but in 1987 for some of the pupae, the short July–August dry season was sufficiently hot to mimic the long dry season, and therefore the September rains were reacted to as though they were the May beginning of the rainy season. *M. dilucida* caterpillars were at least theoretically present in the habitat in the second half of the 1987 rainy season, though I was not able to find any.

Cueing to a temperature change is not restricted to pupae. As clouds build up daily to the south of Santa Rosa, with the May rains approaching closer each day, there are often pulses of cooler air that pass through Santa Rosa before the rains actually arrive. Each night following one of these cool air pulses, enormous numbers of species and individual moths appear at the lights. These moths have obviously been present as adults for weeks to months, and are certainly not cued by rainwater, since none has arrived.

The detailed time of appearance of egg-laying females, and therefore the start of the larval period, is also under selection for adult, egg, and pupal survival and health. This timing is not the subject of this chapter, but it is important to recall that the timing of the caterpillar stage is certainly not a fully independent variable in a selection regime. For example, there may well be tons of highly acceptable foliage and a relatively predator-free microhabitat, yet constraints on adult survival prevent the presence of caterpillars at that time.

#### *Time of Caterpillar Appearance Relative to the First Rains*

Although most species of adult Lepidoptera make their appearance at Santa Rosa (flying or at lights) in the first 2 weeks after the first soaking rains, caterpillars are not abundant nor is their damage readily visible until 3–6 weeks after the first rains. If the first rains are followed by several weeks of dry weather (see below), the delay can be even longer.

There are two obvious reasons for this delay. First, many species of moths and butterflies do not immediately lay all, or even any, of their eggs on foliage as soon as it is available. Rather, they delay their first egg-laying (or eclosion) and therefore spread their egg-laying over several weeks or more. This behavior is probably very functional in those frequent years when the first rains are followed by several further weeks of dry season (e.g., Fig. 14.4). Second, eggs require 5–15 days to hatch; for example, not only do the hemileucine saturniids (*Hylesia*, *Automeris*, *Periphoba*, *Dirphia*, *Molippa*) in Figure 14.6 grow slowly, all their eggs require a full 2 weeks to hatch. Third, many of the small species are at very low density (inconspicuous) and do not become visible in samples or censuses until the second generation emerges; this can be many weeks after the rains, even if the species is one that anticipates the rains and oviposits several weeks before them. Fourth, an enormous number of small caterpillars are taken by predators or killed by the weather before they have a chance to consume enough foliage to be conspicuous through their damage.

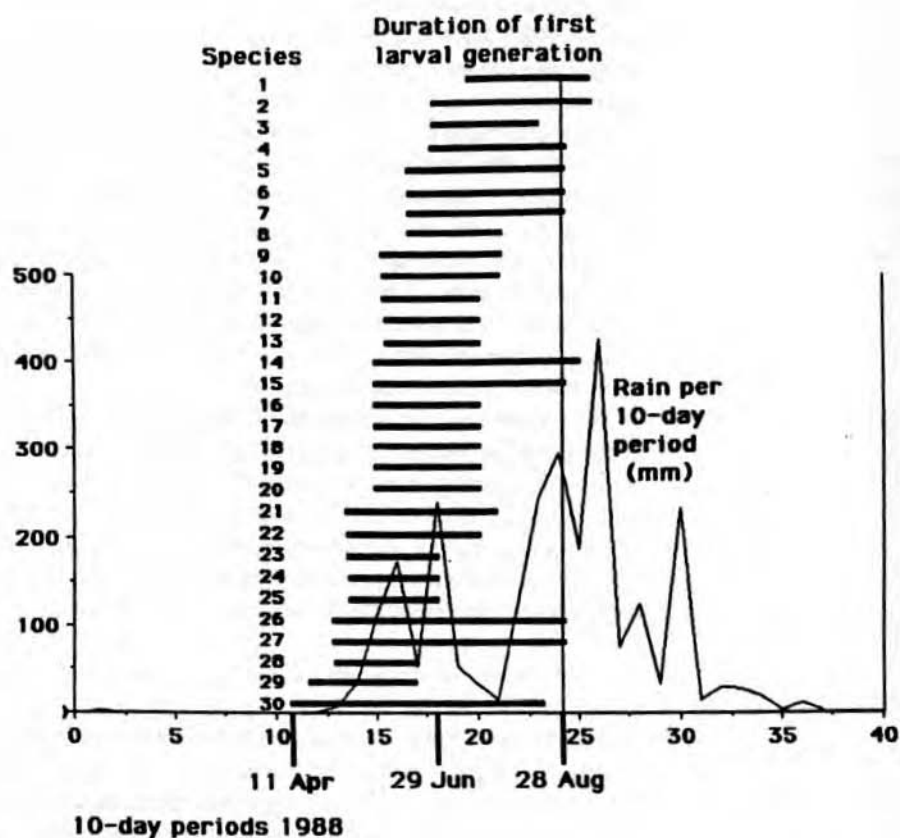


Figure 14.6. The seasonal distribution of the larvae of the first generation of each of the 30 species of Saturniidae that breed in Santa Rosa National Park, ACG, Costa Rica. The date of description of each species is added to emphasize how long the members of this fauna have been known to science (see text). (1) *Automeris io* (1775); (2) *Arsenura armida* (1779); (3) *Syssphinx mexicana* (1872); (4) *Molippa nibasa* (1885); (5) *Hylesia dalina* (1911); (6) *Automeris zugana* (1886); (7) *Automeris zurobara* (1886); (8) *Syssphinx quadrilineata* (1867); (9) *Copiopteryx semiramis* (1775); (10) *Rothschildia erycina* (1796); (11) *Syssphinx colla* (1907); (12) *Titaea tamerlan* (1869); (13) *Citheronia lobesis* (1907); (14) *Automeris metzli* (1853); (15) *Automeris tridens* (1855); (16) *Othorene purpurascens* (1905); (17) *Schausiella santarosensis* (1982); (18) *Citheronia bellavista* (1930); (19) *Caio championi* (1886); (20) *Rothschildia lebeau* (1868); (21) *Eacles imperialis* (1773); (22) *Othorene verana* (1900); (23) *Syssphinx molina* (1780); (24) *Ptiloscola dargei* (1971); (25) *Dysdaemonia boreas* (1775); (26) *Hylesia lineata* (1886); (27) *Periphoba arcaeii* (1886); (28) *Adeloneivaia isara* (1905); (29) *Copaxa moinieri* (1974); (30) *Dirphia avia* (1780).

The consequence of this delay is that a very large number of caterpillars and species of caterpillars do not initiate their feeding on very new, still expanding foliage, but rather on fully expanded new leaves that appear to be fully functional at the time they are eaten. While there are species that feed almost exclusively on very new foliage (e.g., *Eutelia*, *Eulepidotis* and some other noctuids), these species are in the minority. Furthermore, most species that begin their lives feeding on newly expanding leaves in fact can and do eat fully expanded and "mature" leaves as well. It has long been tempting for ecologists to view the caterpillar phase at the beginning of the rainy season as somehow using foliage before it has "hardened up," "matured its defenses," etc. However, in a sample of 80 tree species in Santa Rosa, there was no significant change in the amount of fiber, polyphenolics, or small toxic molecules in the foliage from the time when leaves are generally first fed on (several weeks of age) until very late in the rainy season (6 months of age) (Janzen and Waterman 1984).

Field observations of the overall timing of caterpillar feeding are confounded by feeding by other herbivores. It is commonplace to use the appearance of damaged leaves as a general cue to caterpillar activity. However, Santa Rosa has a rich fauna and high biomass of small melolonthine scarabs that feed on many species of foliage at night. Their feeding damage is characteristic and can be distinguished from that of caterpillars with practice. However, they appear as herbivores from the day of the first rain (or before) and their feeding damage gives the casual observer the impression of much earlier caterpillar activity than is in fact the case.

The dry forest changes from largely brown and leafless to green and fully leafed within a few weeks. Much leaf biomass is therefore aging at somewhat the same rate as the rainy season progresses. However, this does not mean that the larvae present on any given date are consuming leaves of the same age or degree of maturity. First, different species of plants put out their new leaf crop at different times relative to the start of the rains. For example, *Enterolobium cyclocarpum* (Leguminosae) trees flush a major leaf crop 2–6 weeks before the rains, *Crescentia alata* (Bignoniaceae) trees flush a large leaf crop within a week after the first rains, and adult *Hymenaea courbaril* (Leguminosae) makes a new leaf crop in early January, approximately 5 months before the rains.

Second, many species of plants continue to make fewer leaves as the rainy season progresses, both to replace those that have been eaten off and to expand crowns upward and laterally. The ovipositing female has leaves of many different ages among which she can choose, and the caterpillar searching in the crown can also choose among an even greater array of leaf ages during its life. Third, not all conspecifics are highly synchronous in leaf production, even if there is a very obvious seasonal peak. For example, whereas the "evergreen" adult *H. courbaril* trees annually replace their leaf crops in January, small saplings add new leaves throughout the year (with a peak about the time of the first rains in May). Fourth, despite the strong peak of initial oviposition times, many species of moths (or



butterflies) oviposit over a period of weeks to months, thereby creating the possibility of adults and caterpillars being able to choose from among almost every possible leaf age.

Within the early rainy season peak of caterpillar abundance, there is substantial variation among the species within a large taxon. For example, there are 30 species of resident breeding Saturniidae in Santa Rosa. The larvae of all (e.g., Lemaire 1987) can be found within a single square kilometer of late successional dry forest in the eastern end of the park. The earliest eggs to hatch are those of *Copaxa moinieri* and *Dirphia avia* in late April, 2–3 weeks before the rains; the last eggs to hatch are those of *Arsenura armida* and *Automeris io* in early July, a full 6 weeks after the rains have come (Fig. 14.6). Such a spread among a species-rich taxon is commonplace and probably should not be thought of as a detailed evolutionary response to the fine details of the Santa Rosa pre- and post-rains microenvironments. Rather, it is a simple outcome of the various species responding to the weather changes according to whatever cue-response system they had when they arrived at Santa Rosa from other sites and habitats.

It is possible to make a general statement as to when most of the members of the first generation of caterpillars will be present in the habitat (e.g., Fig. 14.6). However, there is great interspecific variation in the degree of response to the various variance-inducing interactions among caterpillars and their habitat. For example, the hemileucine saturniid caterpillars mentioned earlier are much more inclined to increase their caterpillar life span in response to low quality food than are the members of the other three subfamilies. Saturniidae as a group seem to have much more tightly defined caterpillar life span lengths than do Sphingidae as a group (and see Janzen 1984a). Saturniidae as a group have a quite tightly defined pupal period (leading to synchrony of eclosion within and between cohorts in the field), while Sphingidae as a whole are more variable in eclosion times. The consequence is that multivoltine species of sphingids that are nonmigratory during the rainy season (e.g., *Pachylia ficus*, *Protambulyx strigilis*, *Adhemarius gannascus*) tend to have more overlapping generations of caterpillars than do many multivoltine saturniids. However, some species of multivoltine saturniids eclose gradually over a 2-month period at the beginning of the rains (e.g., *Rothschildia lebeau*) whereas others such as *Caio championi* are highly synchronous; again, variation on this point leads to variation in degree of generational overlap.

Finally, I should mention that even within a single higher taxon, caterpillars of the same body weight can have very different development times (e.g., Fig. 14.6). For example, hemileucine Saturniidae can use nearly twice as long to develop from egg to pupa as do other Saturniidae of the same size; this is presumably because the hemileucines are getting substantially fewer nutrients per food bolus than are the members of the more host-specific other saturniid subfamilies (Janzen 1984a, 1985a; Bernays and Janzen 1988). The even more host-specific sphingids display this phenomenon yet more strongly and in at least



one case (*Enyo ocypte* described below) can have two generations in the time that a saturniid of equal body weight has one.

There is a set of moth species whose caterpillars are not tied directly to the weather changes so much as to the flushing of foliage that occurs during the 1–2 months bracketing the first rains. The highly host-specific and stenophagous *Eulepidotis* (Noctuidae: about 30 species in Santa Rosa) is the champion. Two species feed heavily on the very new leaf crops of *Licania arborea* (Chrysobalanaceae), whenever they occur during the last half of the dry season and the first half of the rainy season. The same may be said for the species of *Eulepidotis* that feed on (and sometimes defoliate) the new foliage of *Sloanea terniflora* (Eleocarpaceae), *Sterculia apetala* (Sterculiaceae), *Bombacopsis quinata* (Bombacaceae), *Luehea speciosa* (Tiliaceae), and *Hymenaea courbaril* (Leguminosae) (saplings only). With members of this genus, it is clear that the active adults are present virtually year round in the habitat, but respond to both new foliage and the general time of year to oviposit (there are very few or no *Eulepidotis* caterpillars on new foliage of their hosts during the second half of the rainy season and the first half of the dry season).

#### *The Return of the Killer Dry Season*

As is clear in Figure 14.4, the first heavy rains of the rainy season are not always followed by humid, cool, and moist weather. In at least half of the years, the first rains have been followed by 1–2 weeks of hot and dry weather, nearly as severe as is the dry season in March–April. This is because the first rains are often in response to habitat heating (rising heated air sucking moist air in off the Pacific), and subsequently they cool the habitat enough to stop rain-generating air movements for 1–2 weeks until the environment has heated up again.

When the first rains are followed by dry hot weather, it is commonplace to witness massive mortality of first instar larvae from the eggs laid at the time of the first rains. For example, in 1983, I placed hundreds of first instar larvae of the saturniid *Eacles imperialis* and *Rothschildia lebeau* on their wild host plants in the first rainy week in mid-May. The next week turned dry and hot, and at least 98% of these larvae died of desiccation during this week. They quite obviously could not (or would not) eat enough of the newly expanding foliage to maintain their water balance.

It is not surprising in this context that many pupae of nonfeeding Santa Rosa moths such as Saturniidae, Limacodidae, Mimallonidae, and Bombycidae do not eclose until the rainy season has been present long enough to thoroughly soak both the soil and cool down the general environment. The eclosion dates of moths that can feed as adults (which generally have longer adult lives than do the nonfeeders) do not appear to be so strongly affected, but these moths can delay oviposition until the heavy rains start again.

Different species of caterpillars and different habitats are differentially affected

by an erratically beginning rainy season. In the *E. imperialis* and *R. lebeau* example above, caterpillars on their *Cochlospermum vitifolium* and *Spondias mombin* hosts plants in highly deciduous young secondary succession were all killed, whereas their sibs on the same species of plants in the semishade of relatively primary forest a few tens of meters away displayed moderate survival.

### Migration

One of the most spectacular interactions of caterpillars with seasons in Santa Rosa is the seasonal migration of many species of Lepidoptera back and forth between Santa Rosa and the rainforests to the east of Santa Rosa (Janzen 1984a, 1987a,c, 1988f). About the time of the first rains, more than 100 species of (at least) sphingids, noctuids, nymphalids, and pierids arrive at Santa Rosa (just as they also arrive in other dry forest areas to the south of Santa Rosa). More than 80% of the 64 species of sphingids that regularly breed in Santa Rosa do this. However, in other families, the proportion of migrants is much less. All species of migrants feed as adults and have life spans measured in months.

The migrants have a single generation that occupies 1–3 months of the rainy season (egg–larva–pupa), ecloses, and (mostly) leaves. The adults apparently fly back to the rain forest to the east of Santa Rosa. It is striking that this out-migration occurs in mid-rainy season, at a time of year when the dry forest is humid, cool, and in full leaf (and will continue to be for another 3–4 months). These leaves are clearly edible, as evidenced by occasional larvae of these species that are encountered in the second half of the rainy season. These larvae represent a second generation. They grow at the same rate as do the members of the first generation. These larvae do not show a special predilection for very new foliage, but rather, eat foliage of all ages, just as did their parents' caterpillars in the first half of the rainy season (or, if they specialize on a particular leaf age in the first half of the rainy season, they do likewise in the second half). There is simply no natural history reason to hypothesize that they are leaving Santa Rosa because of inimical weather or a shortage of adult or larval food at the time of eclosion. Ironically, they actually abandon Santa Rosa at its rainiest time of year (e.g., Fig. 14.3, 14.4).

Larval biology interacting with seasonality provides a reasonable suggestion as to why they leave Santa Rosa in August–September. At the time of arrival of the adult moths in late April to mid-May, the carnivore array—spiders, ants, scorpions, bugs, lizards, birds, mammals, fungi, viruses, etc.—is at its lowest point in the yearly cycle, having just endured 6 months of substantial mortality from weather and other carnivores while having no recruitment owing to a general lack of prey. Even the viruses, fungi, and bacteria are at a very low density on the newly produced leaves. The caterpillars—barring a severely irregular start to the rainy season—have a large amount of new and newly mature foliage, high

humidity, and moderate temperatures. Finally, the incoming migrants produce their first dry forest generation in synchrony with all the resident dry forest species that are also having their first generation of the year. There are maximum possibilities for inter- and intraspecific satiation of caterpillar predators and parasitoids at this time of year.

However, when the adults eclose in July–August, they are confronted by a rapidly growing (or risen) carnivore array. This set of carnivores has been replenished by feeding on the large biomass of caterpillars present during the first several months of the rainy season and has benefited by the favorable weather as well. Furthermore, that array is now starving and/or desperate for ovipositional opportunities, owing to the downward plunge of caterpillar density as many species pupate and become dormant, eclose, and remain reproductively quiescent, or eclose and migrate away from the dry forest. These starving carnivores will search extra-thoroughly for prey. At this point in the seasonal cycle, a leafy host plant may have quite ample food but is subject to a living sheet of carnivores. Ironically, if a particular species of plant was mostly defoliated, the few leafy individuals are even more likely to represent lethal concentrations of carnivores, since their leafiness is probably an indication of being within the foraging range of some particularly thorough carnivore (such as a large ant colony) (e.g., Janzen 1985a).

When the adult moth (or butterfly) returns to the rain forest, its offspring do encounter a fierce and omnipresent predator/parasitoid community. It is a moot point as to whether this carnivore array is more dangerous for caterpillars than is the dry forest carnivore array in the second half of the dry forest rainy season. It is tempting to suggest that since they migrate out of Santa Rosa in the middle of the rainy season, the rain forest must somehow be safer than is Santa Rosa at this time. However, evaluating the logic of such a (weak) inference would require a discussion of evolutionary biology of substantially greater size than this chapter (and see Janzen 1985b).

The moths may leave the rain forest for the dry forest in April–May both because the rain forest may be more dangerous (for adults and/or immatures) and because there is more food in the dry forest than in the rain forest after the new leaves have been produced. The intriguing question is whether the rain forest is sufficiently friendly and food-rich for caterpillars to maintain populations of the migrant species if these species were deprived of the dry forest part of their annual biology. I think it likely that the rain forest density of a species steadily declines—even if over several generations—and then is replenished by the incoming brood from the dry forest in August–September of each year.

The above scenarios are substantially influenced by whether the dry forest parasitoid array also migrates to the rain forest. There are some hints that they do. W. Haber (personal communication) has found enormous numbers of hymenopterous parasitoids of caterpillars and eggs at the Monteverde Reserve, a site in AC Arenal at 1400–1800 m elevation on the mountains between Costa Rica's

dry forest and the Caribbean rain forest. These parasitoids are there during the months when it is the late wet season in the rain forest and dry season in the dry forest remnants on the coastal plain and foothills to the east of Monteverde. These wasps appear to be migrating through Monteverde to the Caribbean rain forests, or waiting there in the cool and moist cloud forest habitat, for later return to the dry forest.

A second example is offered by the *Enyo ocypte* sphingid described below. Its pupae are commonly killed by *Belvosia* nsp. 4 (Tachinidae), a large parasitoid that attacks just the sphingids *E. ocypte*, *Eumorpha satellita*, and *Unzela pronoe* in Santa Rosa (*Belvosia* taxonomy, N. Woodley, personal communication). All three of these host caterpillars are available only during the first half of the rainy season. This large fly could easily fly back and forth across the mountains separating Santa Rosa's dry forest from the rain forests that are just a few tens of kilometers to the east. *Belvosia* nsp. 4 has now been reared from *E. ocypte* larvae at Estacion Pitilla, a rain forest biological station in the rain forest northeastern end of Guanacaste National Park in ACG (Figure 14.1). The fly probably does migrate, because it ecloses from the *E. ocypte* pupae in Santa Rosa at the same time as the adult moths eclose (there is no dormancy in the fly puparia). Since there are essentially no host larvae in the dry forest for it to parasitize during the following 7 months, the adult flies have to either survive as adults or migrate. I have not been able to locate adults in Santa Rosa after September and before the following June. Furthermore, when large numbers of the flies are eclosing from sphingid pupae in July, the adults are common in the forest understory. However, they abruptly disappear from that habitat in early August.

There are hundreds of species of Santa Rosa dry forest caterpillar/pupae parasitoids that, like *Belvosia* nsp. 4, eclose in large numbers at the end of the first rainy season generation and then disappear from the habitat (as measured by collections with lights and Malaise traps), only to reappear at the beginning of the next rainy season. As a group, these species must be either hiding, relatively quiescent as adults, or migrating to the rain forest side. If they do migrate to the rain forest, the influx of parasitoids may render the rain forest a yet more dangerous place than it is at other times of year. On the other hand, this will be extremely difficult to study today, if for no other reason than the nearly total destruction of Costa Rican dry forest (Janzen 1988b) will have substantially reduced the numbers of parasitoids to migrate annually.

We do not know to what degree the migrant lepidopterans reproduce in the rain forest. However, there are some hints. There definitely are species that have a second (or more) generation in the rain forests. *Perigonia ilus* provides an example. At the beginning of the rainy season, males and females of this small sphingid arrive at Santa Rosa and oviposit on the new foliage of two rubiaceous trees, *Calycophyllum candidissimum* and *Guettarda macrosperma*. About 2 months later, the adults eclose and leave for the eastern rain forests of Costa Rica (where they are caught occasionally at lights). Of more than 200 rearings of wild

*P. ilus* caterpillars in Santa Rosa, not a single pupa has become dormant (and waited for the next year's rainy season). At the time that they arrived at Santa Rosa (April–May), a sample of 37 adult males caught at the lights had average forewing lengths of 0.327 mm (SD = 0.072 mm), while a sample of 8 newly eclosed wild-caught moths in late June and early July had average forewing lengths of 0.213 mm (SD = 0.057 mm); these differences are significant at the 0.01 level (Janzen 1986a). Although detailed measurements have not been taken, I have observed this difference among *P. ilus* every year (and there are many examples in Costa Rican moths in general where rain forest moths are larger than their dry forest conspecifics). It is clear that the rain forest side of Costa Rica produces bigger *P. ilus* than does the Santa Rosa dry forest. This size differential is of significance here because it demonstrates that there is at least one generation of *P. ilus* on the rain forest side of Costa Rica.

There may be a resident population (in the rain forests) and a migratory population (moving back and forth between the rain forest and the dry forest), or it may be simply that some of the *P. ilus* population "invades" the dry forest annually at the beginning of the rainy season and the offspring return to the rain forest after one generation (a pattern not unlike that of Australian dry forest noctuids, Farrow and McDonald 1987). In either case, there is a background population of *P. ilus* caterpillars present at a very low density in the rain forest throughout the year but a dense population of *P. ilus* caterpillars in the dry forest during June–July. They are a major food item for the trogons to be discussed below.

The very large sphingid *Pseudosphinx tetrio* offers a similar example. This moth appears in Santa Rosa toward the end of the first rainy month. The large aposematic (and/or mimetic) caterpillars (Janzen 1983d) feed only on the leaves and (occasionally) flowers of *Plumeria rubra*. The entire Costa Rican breeding population of *P. tetrio* is therefore restricted to the coasts of both sides of the country, which is the only place that *P. rubra* grows as a wild tree. The last *P. tetrio* larvae disappear from Santa Rosa about the time that *P. rubra* is beginning to drop its leaves in the last month of the rainy season (November). The adults are then (and earlier in the year) encountered at lights throughout Costa Rica's rain forest (from sea level to 2500 m elevation), apparently on their way over to the *P. rubra* trees on the Caribbean coast. Alternatively, these adults may be simply waiting as adults in the inland rain forest until the next May–June. However, there are *P. tetrio* caterpillars on the *P. rubra* trees throughout the year on the Caribbean coast. As with *P. lusca*, *P. tetrio* in Costa Rica may be two populations (one migratory and the other stationary) or one population, some members of which migrate to the Pacific dry forest coast during the rainy season.

The arrival and departure of migratory species can be more complex than meets the eye. The adults may well arrive weeks before their larvae appear in the habitat or they appear at lights. The small sphingid *Enyo ocypete* is an example. Its dry forest food plant is *Tetracera volubilis* (Dilleniaceae). This dry forest large and



woody vine is facultatively evergreen (depending on the amount of shade and soil moisture). However, about a week before the rains begin at Santa Rosa, it begins to produce new leaves in large numbers, and continues through much of the rainy season. About the second week of the rainy season, eggs of *E. ocypete* begin to appear on these new leaves (and adults appear at the lights). A large pulse of *E. ocypete* larvae and pupae pass through development between late May and early August. Almost all *E. ocypete* larvae have disappeared from the *T. volubilis* vines by late July. The pupae from hundreds of wild-caught pupae have never displayed any dormancy. The newly eclosed adults have disappeared from the Santa Rosa habitat by September [they can, however, be collected at flowers in August, apparently gathering food before leaving for the rain forest, where it (and resident conspecifics?) have other generations on the leaves of other dilleniaceae vines].

For 10 years, this appeared to be an accurate description of *E. ocypete* at Santa Rosa. However, in 1990 I found that *E. ocypete* has actually arrived by early April, 6 weeks before the rainy season begins and almost 2 months before the first eggs appear on *T. volubilis* new foliage in the forest. At this time *E. ocypete* lays its eggs on the new foliage of *Curatella americana*, a dilleniaceae tree dotted across the ancient abandoned pastures in Santa Rosa's badly disturbed habitats. The larval generation takes a month. The adults eclose 3–4 weeks later. I cannot know if the new eggs that appear on *T. volubilis* new leaves are from this (first) Santa Rosa generation, or from later incoming migrants, or both. However, since there are two dilleniaceae plants at Santa Rosa that are used by *E. ocypete* during at least part of the year, there are two distinct peaks of caterpillar density—with each peak representing the initial pulse of new leaves by the host. It is particularly striking that both host plants continue to produce new leaves throughout the rainy season, but neither these new leaves nor the older new leaves are used by *E. ocypete*, except for a very few very rare individuals (probably from eggs from the few adults that do not migrate out of Santa Rosa until the second half of the rainy season). During the normal caterpillar season, the caterpillars feed on *T. volubilis* and *C. americana* leaves of all ages (though they begin on new expanding leaves, where the eggs are laid).

There are many ways in which forest clearing or alteration can change the dynamics and demography of dry forest caterpillars or migrants. The *E. ocypete* interaction with its hosts offers an example. In the pre-European Santa Rosa habitat, *C. americana* would have been a very rare and local tree, restricted to rocky outcrops and other areas where the forest canopy does not naturally exceed about 5–10 m height. It could not have been but a quite trivial host for *E. ocypete*, as compared to the common *T. volubilis*. The latter plant is common in Santa Rosa dry forest of all kinds and ages—from deeply shaded understory to full insolation. It is possible that *E. ocypete* has always arrived in April in Santa Rosa and simply waited—while feeding at flowers (?)—for *T. volubilis* to reach the appropriate stage for oviposition in late May–June. However, with forest clearing



and the very great expansion of the *C. americana* population in low-grade and frequently burned pastures, this new and earlier food source can probably absorb much of the egg-laying potential of the incoming *E. ocypete* population. It is not possible to know, however, whether this generation on *C. americana* results in a yet higher density of offspring *E. ocypete* caterpillars on *T. volubilis*. It is quite striking, however, that the newly eclosed adults in May oviposit only very rarely on the *C. americana* new leaves being produced at that time.

### Univoltine Nonmigrants

The migrant Lepidoptera described above are largely univoltine as far as Santa Rosa is concerned. There is also a large and taxonomically more diverse group of univoltine species that do not migrate (Janzen 1987a). Instead of eclosing and flying out of the habitat, in effect the caterpillars put themselves in tight cocoons, tough pupae, and/or underground chambers and simply wait out the second half of the rainy season and all of the dry season. *Manduca dilucida* is a dry forest sphingid mentioned earlier that behaves in this manner. Interestingly, *M. dilucida* have life spans of only several weeks duration—exceptionally short for feeding sphingids—and carry large numbers of seemingly mature eggs when they arrive at lights—a very saturniid-like trait. *Schausiella santarosensis*, the only saturniid endemic to the Santa Rosa area, has a similar biology.

It is significant in this context that even if the carnivore intensity during the second half of the Santa Rosa rainy season fluctuates from year to year, the univoltine species—migrants and dormant pupae or prepupae—will not be aware of it, and their populations at the beginning of the following rainy season generation will not reflect it (except with respect to predation by extreme generalists such as armadillos and mice that dig up hidden pupae).

### An Example of Caterpillar Predation by Vertebrates

The extreme seasonal and annual fluctuation in caterpillar abundance in Santa Rosa dry forest appears to be a major component of the biology of those vertebrates that feed on caterpillars. This is not, however, a simple thing to interpret. I offer the nesting biology of the elegant trogon, *Trogon elegans*, as an example. This medium-sized bird is common in Santa Rosa dry forest and its nestling feeding biology is the subject of an on-going multiyear study (F. Joyce and D. H. Janzen).

*T. elegans* nests in holes in tree trunks. During the first several weeks of the rainy season, *T. elegans* pairs locate nest holes and incubate eggs. By placing a soft but tight collar around the nestlings' necks, the nestlings are prevented from swallowing the caterpillars (or other food items) brought by the parents. The food

is then collected by the observer, the collar removed, the nestling given an alternate and equivalent food item, and the collar replaced. During the past 5 years, data obtained in this manner from 1584 feeding events at 22 *T. elegans* nests in Santa Rosa allow the following general conclusions.

The timing of nestling appearance is such that by the time the nestlings are begging for food, the habitat is rich in the last instar caterpillars of Sphingidae (as well as a variety of other large insects). In a "normal" year, last instar sphingid caterpillars constitute about half of the nestling diet in numbers of individuals brought in, and as much as 70% of the nestling diet in biomass. The remaining diet is pure insects, except for an occasional spider or anolis lizard (*Anolis* or *Norape* spp.). More than 98% of the sphingid caterpillars are in their last instar, irrespective of whether they belong to a small, medium-sized, or large species of sphingid. By about the end of July, the density of last-instar sphingid caterpillars in the forest has declined to a very low level. At the very few remaining (or new) nests at that time, other insects (mostly last-instar saturniid and notodontid caterpillars, and Orthoptera) become the major food items. For the remainder of the rainy season, and all of the dry season, there are no further nesting attempts by *T. elegans*. In the first 3 years of the study (1986–1988), this was the pattern, and it was easy to come to the global conclusion that the presence of a *T. elegans* breeding population in Santa Rosa was dependent on the peak of last instar caterpillars of large moths during a 2-month period that begins about 2 weeks after the beginning of the rainy season.

However, in 1989, a natural experiment occurred. The density of sphingid caterpillars in Santa Rosa declined dramatically. The seasonal peak in larvae disappeared (for quite inexplicable causes). For example, in 1988, sphingid larvae constituted 40.2% of all caterpillar collection records in the Santa Rosa caterpillar inventory ( $n = 614$ ); in 1989, only 8.3% of the collection records by the same collectors collecting in the same habitat were sphingids ( $n = 919$ ). The *T. elegans* responded to this decline in sphingids by feeding their nestlings more caterpillars of other species of insects. For example, sphingids made up 49.6, 49.6, 50.7, and 45.6% of the nestling diets in 1986–1988 and 1990, respectively, but only 23.3% in 1989 ( $n = 133, 232, 493, 338, \text{ and } 388$  in consecutive years). I should add that for the adult trogons to find even this high a percent of sphingids required diligent and directed search for sphingids, since sphingid larvae were far more than 50% reduced in density in Santa Rosa in 1989. In addition, the trogons brought fruit to their nestlings in 1989 (adults trogons eat fruit regularly). For example, 19.5% of the food items in 1989 were fruit, while no fruit were brought in 1986–1988 and 1990.

It is not presently possible to know if permanent removal of the sphingid caterpillars would result in the elimination of *T. elegans* from Santa Rosa or simply produce a change in their nestlings' diet. The fact that they do not breed during the second half of the rainy season (when there are abundant orthopterans, a few other large caterpillars, and some fruit) suggests that the sphingids are a

critical resource. However, the fact that they can shift to other food items when sphingid caterpillars are scarce (as in 1989) demonstrates that the sphingids can be interchanged with other items. It does not, however, demonstrate that a breeding population can be maintained without the abundance of food represented by the normally high density of sphingid caterpillars in the first half of the rainy season. The ability to interchange sphingids for other food items appears to be contradictory to the observation that they breed only during the part of the rainy season in which sphingids are present. It is tempting to suggest that the sphingid caterpillars offer the best nestling growth and/or are optimal for adult foraging regimes, but substitutes are acceptable (with perhaps lowered survival or health of the fledged young). In this scenario, it is implied that the second half of the rainy season neither has the sphingid caterpillars nor sufficient alternative foods for nesting, and/or the second half of the rainy season is (also) inimical to nesting *per se* (e.g., due to an abundance of predators, or due to producing fledglings so close to the dry season that they do not have time for whatever development is necessary for dry season survival).

Unfortunately, there is an awkward alternative hypothesis, based on the concept of "ecological fitting" (Janzen 1985b). This would be that *T. elegans* is genetically locked into breeding only during the first half of the rainy season wherever it is, and feeds its nestlings whatever its genes view as the best food. If sufficient food is present, the population persists; if the food is insufficient, the population is not established. In this scenario, the fact that sphingids make up a large part of the nestlings' diet is a simple reflection of the adults' choice/priority/ability during the time of year when they nest, but does not demonstrate that they are contemporarily basing their nesting phenology on the sphingid caterpillar peak in abundance, or that the Santa Rosa sphingid caterpillar seasonal presence was part of the selective regime that generated or maintains this nesting phenology.

### Aseasonality

The most "aseasonal" externally feeding caterpillar in the study site is *Hypercompe icasia* (*Epantheria icasia*), a large arctiid whose caterpillar resembles the "wooly bear" of the northern United States. It appears to be rejected by all vertebrate predators. This caterpillar is an extraordinary generalist in its diet (Janzen 1988d). An individual caterpillar feeds for a few minutes to hours to days on a particular plant, and then walks on by ground or foliage to other plants, where it may feed as well. It does not eat all species that it encounters, but it does have a host list of more than 70 species of woody plants to date. Many, but not all, of the plants that it eats can serve as an adequate diet to pupation if the caterpillar is restricted to them in the penultimate or ultimate instar. I have found active and feeding last instar larvae in all months of the year. *H. icasia* is extraordinarily slow growing for two reasons. First, it can easily starve for as

long as 1–2 weeks without feeding. Second, even when confined to a seemingly high-quality food (which it eats in copious amounts), it grows more slowly than do the slowest and most generalist hemileucine Saturniidae (e.g., *Hylesia lineata*, Janzen 1984c). It is commonplace for a *H. icasia* caterpillar to use 2–3 months on a mixed or pure diet before pupating. The pupae eclose after about 16–20 days and even during the dry season show little inclination for delayed development.

It appears that the world is not covered with *H. icasia* because when the females lay their batches of hundreds of very small eggs during the dry season, the very small first-instar larvae have very low survivorship at that hot, windy, dry and largely leafless time of year. The very few that survive to become adults at the beginning of the rainy season produce a highly variable number of last-instar larvae by August. For inexplicable reasons, the adults that eclose in August–September do not generate abundant last-instar caterpillars by the end of the rainy season (November). *H. icasia* are often the last large and conspicuous caterpillars to be found in Santa Rosa as the dry season intensifies in December–January.

There are numerous species of evergreen trees, shrubs, and vines in Santa Rosa's deciduous forest. Many of these are host to many species of caterpillars during the rainy season, but none is a host plant to external feeders year-round. In general, even those species of Lepidoptera that have multiple and overlapping generations feeding on these plants during the rainy season do not also feed on them during the dry season. For example, the caterpillars of the large nymphalid butterfly *Archaeoprepona demophoon* are occasional to common (depending on the year) on the understory evergreen treelet *Ocotea veraguensis* (Lauraceae) from about the time that the rains begin until the first month of the dry season. The adult butterflies, however, are present in the habitat throughout the year. They do not oviposit on their sole host in Santa Rosa during the dry months, even though the host plant is fully covered with leaves of all ages.

### One-Liners

Space limitation does not permit elaboration on all the patterns that are beginning to emerge in caterpillar phenology associated with the seasons in Santa Rosa dry forest. However, it may be useful to briefly mention some. For example, it is at the end of the rainy season that leaf-mining lepidoptera constitute the largest proportion of the active leaf miners (J. Memmot, personal communication). This may well be due to leaf miners being poor at dormancy (owing to their tiny size) and their populations therefore being severely depressed by the dry, hot, and leafless dry season.

Butterfly caterpillars (Heperioidea, Papilionoidea) as a group show the same phenological patterns as do externally feeding moth caterpillars as a group. Santa Rosa butterflies have highly migratory species with a phenology virtually identical

to that of many sphingids (e.g., the nymphalids *Marpesia chiron*, *M. petreus*, the pierid *Aphrissa statira*), dormant largely univoltine species (e.g., the papilionids *Eurytides philolaus*, *E. epidaus*, *Papilio astyalus*), species that are reproductively dormant but active as adults during the dry season (e.g., many Hesperidae, the nymphalid *Siproeta stelenes*, the pierid *Eurema daira*—and see Odendaal 1990; Jones 1987), etc.

There are many species of small moth caterpillars that live inside of fruits [e.g., *Ectomyelois muricis* (Phycitinae) in *Hymenaea courbaril* fruits, Janzen 1983c], rolled leaves (e.g., tens of species of pyraustine Crambidae), seeds (e.g., the Mexican jumping bean moth, *Cydia deslaisiana*, Olethreutidae; det. J. A. Powell), flowers [e.g., *Margaronia venatalis* (Pyraustinae) in fallen flowers of *Stemmadenia obovata*,] etc. With rare exceptions, none of these larvae displays any kind of dormancy as pupae or prepupae, and the pupae are not desiccation resistant at Santa Rosa temperatures and dry season humidities. As nearly as I can determine, most of these small moths pass the dry season as quiescent and hiding adults (Janzen 1987a) just as do many butterflies (Odendaal 1990; Jones 1987). It is particularly striking that if there is an aseasonal heavy rain in the middle of the dry season, or if cool weather appears for a week or so before the actual rains, adults of many of these species appear at the lights in forest that is leafless, dry, hot, and windy by day.

Although many moths and butterflies display quite uniform periods of duration of the pupal stage during the rainy season, there are a smattering of species that are extremely irregular with respect to this trait. This leads to quite irregular appearance of caterpillars of these species after the first generation of caterpillars following the rains. Various species and genera of Noctuidae, Arctiidae, and Thyrididae are particularly likely to have pupae that eclose after quite unpredictable intervals of weeks to months. Study of this phenomenon is particularly difficult, however, because it is never clear whether laboratory conditions have allowed or generated the eclosion cues used by the pupae.

Not all caterpillar phenology is as one would predict from the weather. Cossidae are the most startling. Adult cossids, which do not feed and therefore lay their eggs within a few days, appear at the lights in largest numbers (species and biomass) in the first month of the dry season (January). This seemingly nonsensical behavior may be related to the extreme windiness in January–February, a windiness that creates frequent wounds in living tree trunks through breaking and falling branches and trees. I suspect that many first instar cossid larvae gain entrance to the tree bark or trunk through these wounds. Additionally, once inside the living tree trunk, cossid larvae are probably the best shielded from the heat and desiccation of the dry season of any group of feeding caterpillars. Other exceptions are caterpillars that are specialists at mining in medium-sized fruits and seeds, many of which are produced only during the dry season at Santa Rosa. For this group of moths, it is clear that the rainy season is the inimical season, just as is the case with bruchid beetles (Janzen 1980b), spiny pocket mice (Janzen



1986b), and other dry forest seed predators (e.g., Janzen 1989b). At this point it should also be emphasized that not even all of the rainy season has physical conditions suitable for some groups of caterpillars. The short dry season in the middle of the rainy season is obviously a time of difficulty for first-instar larvae of external feeders. However, the aquatic caterpillars (e.g., nymphuline Crambidae) at Santa Rosa often find flowing water in the streams only during a few weeks to a month during the entire rainy season.

### **In Closing**

Santa Rosa dry forest caterpillars clearly respond to and/or are affected by the seasonality of a wide variety of abiotic and biotic traits of their forest. My experiences in other dry tropical forests in Mexico, Guatemala, Venezuela, Australia, Kenya, Uganda, and India all suggest that the Santa Rosa situation is generally representative.

I do not see any evidence that there are new major ecological and evolutionary principles to be unveiled in tropical dry forest any more than in tropical rain forest. Of greater importance is coming to understand ecological, behavioral, and physiological interactions in such a manner that the information will be useful in allowing human management, manipulation, conservation, and use of these complex ecosystems without destroying them. For example, seasonal migration of Lepidoptera is hardly a new concept in biology. However, conservation planning can certainly make use of the fact that a conserved tropical dry forest needs to have some kind of sister rain forest area for its migrants to move to during the dry season. A budding butterfly farm industry can certainly make use of pupal dormancy as part of its manufacturing regime. It is difficult to plan tropical grade school exercises with caterpillars as the subjects (e.g., Janzen 1989a) in an area where no caterpillars are readily available for 8 months of the year. The seasonal timing of caterpillars and their parasitoids will definitely influence the planning of dry season irrigation of crops and tree plantations. Research on these considerations and many more like them needs to be done to bring tropical conserved wildlands into productive harmony with the remainder of tropical society.

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