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HOW MOTHS PASS THE DRY SEASON IN A COSTA RICAN DRY FOREST

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Abstract—The dry and largely deciduous forests in Santa Rosa National Park in northwestern lowland Guanacaste Province, Costa Rica, Central America, have a moth fauna of about 2800 species. These moths pass the six month rain-free dry season, and some other portions of the year, by: (a) remaining dormant in the egg stage (1 species only), (b) remaining dormant in the pupal or prepupal stage (many species), (c) undergoing larval development (a few species of particular life forms) (d) remaining in the Park as a potentially active but non-reproductive adult (many species), and (e) migrating out of the Park after one to two generations and then returning at the beginning of the following rainy season (a few species of particular life forms). The migrating moths constitute a strong link between the dry forest and the rainforests to the east of the dry forest. The seasonal patterns of dormancy of immatures, reproductively dormant adults, and migration are not well correlated with the simple presence or absence of foliage on host plants, or with climate changes (except that the temperature drop that occurs at the beginning of the rainy season appears to be a widely used cue for pupal eclosion). The pattern of habitat use by leaf-eating caterpillars is probably determined more by the seasonal abundance of carnivores (parasitoids and predators) than by the mere presence of leaves; this process is very strongly evident in the failure of many moths to have more than one generation per year, even when their host plants are leafy throughout the six month rainy season or are even evergreen.

Key Words: Moths, dry season, seasonality, Costa Rica, Neotropics, migration, dormancy, pupae, rainforest, dry forest, Santa Rosa National Park.

Résumé—Les forêts arides à feuilles caduques du parc national de Santa Rosa dans le nord-ouest de la province de Guanacaste, Costa Rica, Amerique centrale, ont une faune de mites d'environ 2800 espèces. Ces mites passent les six mois de la saison sans pluie et une autre partie de l'année en: (a) restant dormant d'espèces), (c) se développant en larves (peu d'espèces), (d) restant dans le parc sous forme d'adultes ayant une activité potentielle mais non reproductive, et (e) migrant hors du parc après une ou deux générations puis retournant lors de la prochaine saison des pluies. (peu d'espèces). La migration des mites constitue un retournant lors de la prochaine saison des pluies. (peu d'espèces). La migration des mites constitue un maillon important liant les forêts arides et les forêts humides. Les modèles saisonniers (les immatures dormants, adultes dormants qui peuvent se reproiduire) et la migration ne correspondent pas bien avec la présence ou l'absence des feuilles sur les plantes hôtes ou avec les changements du climat. (A l'exception de l'éclosion des pupes qui elle semble correspondre à la chute de température au commencement de la saison des pluies.) Le mode de vie des chenilles qui mangent les feuilles est propablement limité par l'abondance des carnivores (parasitoids et prédateurs) et non par l'abondance des feuilles. Cette régulation est évidente pour beaucoup de mites qui ont plus d'une génération par année, même si les plantes hôtes portent des feuilles pendant les six mois de pluie ou même si les arbres ont des feuilles persistantes.

INTRODUCTION

Santa Rosa National Park has an estimated moth fauna of about 2800 species (Table 1; cf. Janzen, 1987a). The 108 km^2 Park covers a small coastal plain and adjacent mesa (0–350 m elevation) in Guanacaste Province in northwestern Costa Rica (Boza and Mendoza 1981; Janzen, 1986a). It has a 6 month rain-free dry season (late November or early December through late April or early May) and a rainy season during which there is about 1–2 m of rain distributed in two major peaks (Table 2). The original forest cover contained approximately 700 species of angiosperms (Janzen and Liesner, 1980) and varied from totally deciduous forest on rocky ridges to semi-evergreen forest in moist canyons. Today, this forest cover is a mosaic of various ages of secondary succession that ranges from abandoned grass pastures to 400-year-old forest. There are even a few hectares here and there of the original forest, from which only a few individual trees have been removed (Janzen, 1986a).

Santa Rosa's large fauna of moths is unambiguously a tropical dry forest fauna. However, many of them have geographic distributions that cover tens of degrees of latitude (Janzen, 1987b). Even within Costa Rica, many of these species occur in rainforest as well as dry forest. A major ecological question is how these moths survive the Santa Rosa dry season, a time of year that is sufficiently dry that most larval foods disappear. Here, I briefly outline some of the more common ways that they pass the dry (and some other inimical) seasons, but recognize

Table 1. The Lepidoptera fauna of Santa Rosa National Park, Guanacaste Province, Costa Rica (0–350 m elevation, 11° N Latitude). These figures are based in part on a butterfly checklist (DeVries, 1983) and primarily on field collections at lights and rearing in Santa Rosa from 1978 to 1986 (cf. Janzen, 1987b). These figures should be discounted by about 3% to eliminate species richness added by strays

Insects	Numbers
Butterflies	345
Arctiidae *sensu latu*	90
Lymantriidae	5
Limacodidae	20
Cossidae	25
Sphingidae	84
Saturniidae	35
Mimallonidae	8
Apatelodidae	10
Lasiocampidae	5
Geometridae	400
Notodontidae	150
Noctuidae	800
Microlepidoptera	1130
Miscellaneous	35
Total Lepidoptera	3142

that more ways will become evident as the natural histories of these moths become more thoroughly understood.

MATERIALS AND METHODS

This study began in 1978, at which time massive collections and censuses of moths at lights were initiated and maintained through 1985 as a way of determining what moth species actually occur in the Park. The lights were placed in and above the forest throughout the year, and the moths that came to them observed and collected. The rate of accumulation of species of macro-moths new to the collection from the lights had fallen to a level of approximately five per year by 1985 (microlepidoptera have been extensively collected, but are not sufficiently well-studied to determine if the rate of accumulation of new species differs significantly from this). Simultaneously, more than 5000 rearings of wild-caught caterpillars have yielded over 500 species of moths; all but one of these have also been caught at the lights placed out in the forest in the Park. Identification of these moths and the preparation of field guides (e.g., Janzen, 1982) and reference collections is an on-going process involving a large network of moth taxonomists, without whose efforts the study would not be possible.

During the above survey of the species and natural history of Santa Rosa moths, numerous observations have been made on the seasonal behaviour of particular species and some species have also been examined through experiments on seasonality. Here I briefly describe some fragments of Santa Rosa moth natural history, more extensive accounts of which will be published elsewhere (e.g., Janzen, 1983; 1984a–c; 1985). Where relevant, methods associated with particular examples are presented in the text. Much of the choice of examples is dictated by the availability of names rather than by what is known to date. All names used here are those currently favoured by the specialists in a particular group, and are backed by voucher specimens at the University of Pennsylvania.

Santa Rosa eggs, prepupae and pupae either pass onto the next developmental stage within a few weeks or remain in a state of apparently arrested development for a period of months. Throughout this essay I refer to immatures in the later state as 'dormant' or as being in a state of "dormancy", with no intended implication as to the physiological mechanisms or cueing systems involved.

RESULTS

There are five conspicuous ways that Santa Rosa moths survive the dry season:

(i) Remain dormant in the egg stage.

(ii) Remain dormant in the pupal or prepupal stage.

(iii) Undergo larval development.

(iv) Remain in Santa Rosa as a potentially active adult.

(v) Migrate out of the Park (and dry forest) to the wetter (evergreen) parts of Costa Rica and return at the beginning of the subsequent rainy season.

All five of these life styles are relatively discrete, but there is some overlap among the last four within some species.

(I) *Remain dormant in the egg stage*

Only one species of moth, *Hylesia lineata* (Saturniidae) is known to pass the dry season in the egg stage at Santa Rosa (Janzen, 1984b), and no other Santa Rosa moth has an adult biology that suggests that the species survives the dry season as dormant eggs. The eggs that will pass the dry season are laid in a ball and covered with a felt made of the female's abdominal hairs. This oviposition occurs in late December to early January. The larvae emerge about the time of the first soaking rains in early May. A generation uses about three months. The eggs for the second generation (August–September) hatch within several weeks of oviposition. It is the eggs laid by the adults emerging from the second generation

Table 2. Monthly precipitation (rounded to the nearest mm) in the administration area of Santa Rosa National Park, Guanacaste Province, Costa Rica (data collected by Park Rangers, and extracted from the Meteorology Institute in San Jose)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1980	1	0	5	0	184	175	139	159	331	417	240	9	1660
1981	0	1	1	11	353	582	172	478	195	268	153	27	2241
1982	16	2	0	41	919	129	117	34	328	197	37	1	1820
1983	2	0	22	4	21	180	106	107	188	201	79	7	917
1984	6	8	0	0	118	218	278	162	613	261	52	7	1723
1985	0	0	0	3	99	211	154	169	214	436	119	26	1431

(December–January) that are dormant and pass the dry season. *H. lineata* pupae never enter prolonged dormancy in the field or laboratory (under ambient conditions); they eclose after 2–3 weeks no matter what time of year they are formed. This life cycle is reflected in the pattern of appearance of *H. lineata* adults at lights in Santa Rosa; it is unique in that adults do not appear at the beginning of the rainy season (late April through May), but instead first appear at lights towards the end of July (when other large moths are also emerging from the pupae of their first generation).

The other species of *Hylesia* at Santa Rosa, *H. dalina*, lays its eggs in a layer on a leaf surface and only lightly covers them with hairs. Its eggs always hatch within 2–3 weeks of oviposition, and most of the pupae remain dormant through the dry season. *H. dalina* is like the other 28 species of Santa Rosa resident saturniids that survive the dry season as dormant pupae.

(II) *Remain dormant in the pupal or prepupal stage*

A large proportion of the species of moths in Santa Rosa pass all or part of the dry season as dormant pupae or prepupae. In addition, the pupae of numerous species are also dormant for extended periods during the rainy season. Many of the patterns of pupal dormancy do not correlate well with a concept of a simple six month dry season and a six month wet season. Much more research on pupal dormancy of Santa Rosa's moths is needed before the biology of the patterns can be understood in general terms, but some tantalizing fragments of the patterns are already evident. Furthermore, there are some non-obvious aspects of pupal biology in a tropical dry forest that are worth brief exploration here.

(1) *Patterns of voltinism.* (a) *Univoltine species.* There are numerous species of non-migratory Santa Rosa moths that are entirely or almost entirely univoltine. Such species spend at least 10 months of each year as dormant pupae or prepupae. Below I briefly describe the life cycles of five of them.

(i) Schausiella santarosensis (*Saturniidae: Ceratocampinae*). This medium-sized saturniid ecloses in May, within 1–2 weeks of the date when the rains at the beginning of the rainy season (Table 2) have been sufficiently heavy to soak the soil surface. The females lay their eggs in the crowns of 10–30 m tall *Hymenaea courbaril* (Leguminosae) trees; the solitary larvae eat fully mature leaves and use 4–5 weeks to develop. The larvae drop to the ground, construct their pupation chambers in the upper 1–2 cm of the soil just beneath the litter, and pupate within 3–4 days. About 99% of these pupae then remain dormant until shortly after the rains come again in the following May.

This percentage is based on three observations. First, of the pupae placed in wet and dry conditions in the laboratory at Santa Rosa under approximately ambient temperatures, only about 1% eclose during the rainy season in which they pupated. Second, *S. santarosensis* arrives readily at lights that have been placed in *H. courbaril* forest. During the May emergence period, 10's to 100's arrive per light month (= a light maintained nightly for a month at a site in the forest), but during the remainder of the rainy season, only 0–1 arrive per light month. Third, while the larvae are abundant in the crowns of *H. courbaril* in June and early July, none have been located during the remainder of the wet season despite intensive search in the *H. courbaril* crowns and search for the distinctive large fecal pellets on the ground beneath the trees.

The pupae of *S. santarosensis* are therefore dormant as pupae through the central third of the wet season (this period—locally termed the "veranillo"or "little dry season"—ranges from almost rain free to very rainy (Table 2), the terminal third (and very wet) portion of the wet season, and the 6 months dry season. Throughout this period, the evergreen host plant bears a full crop of mature leaves except for about 2 weeks in late December or early January when its old leaf crop is dropped and a new one flushed out. I have obtained one fecund female *S. santarosensis* from the "second generation" (the 1% or less of the pupae that eclose during the same rainy season as they pupated) and her offspring grew normally to healthy and dormant pupae on *H. courbaril* foliage in August and September. There is no suggestion that the absence of a second rainy season generation or a dry season generation is due to decreased food quality at these times. Rather, I suspect that, just as with other Santa Rosa foliage-eating caterpillars that have only one generation per year, they restrict the caterpillar portion of the life cycle to the time of year when the carnivore (parasitoid and predator) density is lowest.

(ii) Manduca dilucida (*Sphingidae*). This medium-sized sphingid ecloses about a week after the soil is heavily soaked by the first rains of the rainy season (usually the first half of May). The adults arrive at lights by the tens per light-night for about 20 days, after which they disappear totally from the lights for the remainder of the year. Likewise, the adults appear at flowers only during the 3 weeks that they arrive at lights. The solitary caterpillars are common on their several species of host plants (*Sapranthus palanga* and *Annona reticulata*, Annonaceae; *Rehdera trinervis*, Verbenaceae; *Cordia alliodora*, Boraginaceae; *Tabebuia ochracea* and *Crescentia alata*, Bignoniaceae; and others) during June. They consume foliage of all degrees of maturity, though none of the leaves that they eat is older than 1–2 months (all of their host plants are deciduous). The larvae then burrow down through the soil to a depth of 5–15 cm, construct their smooth-walled ovoid pupation chambers, and pupate within 4–6 days after leaving the host. The pupae then remain dormant until the beginning of the rainy season of the following year.

There are no natural history observations to suggest that a portion of the *M. dilucida* population furtively ecloses during the rainy season and migrates out of the area. There is other evidence to support the contention that there is only a single generation per year. For example, the caterpillars have been found only between late May and early July. In Costa Rica, the moth is known only from the dry northwestern portion of the country (roughly speaking, lowland Guanacaste Province and extreme northern Puntarenas Province) and captures from lights at other sites display the same phenology as at Santa Rosa. *M. dilucida* pupae are therefore dormant, deep in the soil, throughout a 4 month period of the wet season, a period when all of their host plants are bearing full leaf crops and the soil around them is wet. They are also dormant during the dry season, a time when their larval host plants are leafless or losing their leaves. *M. dilucida* has only one large ichneumonid parasitoid *Tricyphus respinozai* I. Gauld, pers. commun.), and this wasp remains dormant as a pupa inside the *M. dilucida* pupa throughout the period that the pupa is dormant. However, it ecloses approximately two weeks after the moth does; this means that immediately after the eclosion of the wasp, there are *M. dilucida* caterpillars available in which to oviposit.

When over a 100 pupae were placed in dry and wet plastic bags in a laboratory under approximately ambient temperature conditions at Santa Rosa, all of them remained dormant throughout the cycle of the seasons and eclosed in synchrony with their wild conspecifics the following year. However, when a batch of *M. dilucida* pupae were mailed to the US and subjected to a variety of unknown (put probably chilling) temperature regimes, some eclosed only 1–5 months after pupating.

(iii) *near* Thyrinteina *new species* (*Nacophorini, Geometridae*). This medium-sized geometrid is common at the lights from as early as a week before the first rains through the time of the very first heavy rains. It then disappears from the lights for the remainder of the year. During late May and the first half of June, the caterpillars are common on saplings of the deciduous trees *Casearia corymbosa* (Flacourtiaceae) and *Rehdera trinervis* (Verbenaceae), and are found occasionally on some other deciduous woody plants as well. In the laboratory at Santa Rosa, the mature caterpillar spins a very tough silk cocoon in litter, remains as a dormant prepupa until April, pupates, and then ecloses about the beginning of the rains in the following year. Cocoons placed in dry and wet plastic bags in the laboratory at Santa Rosa did not generate moths until the beginning of the wet season of the following year. Additionally, cocoons of this species brought in 1985 to Philadelphia from the extremely dry forests of western Mexico at the Chamela Biological Station, generated moths in late April–early May 1986 in dry plastic bags; however, the temperature regimes to which these pupae were subjected are unknown (A. Pescador, pers. commun.).

(iv) Neogalea sunia (*Noctuidae*). This medium-sized noctuid is common at the lights for about 1–2 weeks after the rains begin. It then disappears from the lights for the remainder of the year. The caterpillars are common on saplings of the deciduous tree *Rehdera trinervis* (Verbenaceae) during late May and the first half of June. The mature caterpillar spins a very tough silk cocoon on the sides of twigs and stems of the host, pupates within a few days, and then remains dormant until the beginning of the rains in the following year. Cocoons placed in dry and wet plastic bags in the laboratory at Santa Rosa did not generate moths until the beginning of the wet season of the following year.

(v) Macalla thyrsisalis (*Epipaschiinae, Pyralidae*). This medium-large pyralid is common at the lights for about 2 weeks after the rainy season begins. It lays its eggs on the new foliage (1–3 weeks old) in the crowns of large adult *Cedrela odorata* (Meliaceae) trees. The solitary larvae web and partly roll up the terminal leaflets of the host plant's large compound (deciduous) leaves and are on the plant 2–3 weeks. The mature larva drops off and spins a tight cocoon among the leaf litter, in which it then remains as a quiescent pre-pupa (quiescent larva) for the following 10.5–11 months. During this period, if a cocoon is cut open, the larva repairs the cocoon by spinning new silk over the cut. About the time of the first rains in April, or perhaps 1–2 weeks before, the larvae pupate and the adults eclose 1–2 weeks later. The larvae display the above behaviour in the laboratory at ambient temperatures and in either wet or dry containers.

(b) *Multivoltine species*. At least half of the species of Santa Rosa moths have a complete generation within the first 1–2 months after the rainy season begins, pupate for 2–8 weeks, eclose and then repeat the cycle one, two or three times. At the end of the second, third or fourth caterpillar generation, the cycling stops and the pupae remain dormant until the second half of the dry season (see below) or the beginning of the rainy season of the next year. Additionally, in some species a portion of the population remains as dormant pupae after the first (or second or third) generation, and a portion continues to have generations until a later date. Just as is the case with seed dormancy, the pattern of pupal dormancy displayed by laboratory populations can be very difficult to relate to the pattern in the wild. Worse, the dormancy behaviour displayed by a pupa in the laboratory may almost never occur in the field. For example, the amount of time that a pupa will stay dormant under laboratory conditions may be quite artificial if in the field the ambient conditions always lead to eclosion. The direct parallel occurs with dry forest tree seeds that survive for years on herbarium sheets, but always germinate within a few years in the soil in the wild.

Change in the ambient conditions associated with the beginning of the rainy season cues many species of adults to eclose, whether they have been dormant for a long or a short period. This means that cohorts and populations that have been drifting out of synchrony during their successive generations during the rainy season are brought back into synchrony by their pupal dormancy during the up-coming 6 month dry season.

The large saturniid moth, *Arsenura armida* has two semi-overlapping generations and offers a (somewhat problematical) example. In 1985, more than 100 last instar first-generation larvae were collected from their host plants (*Bombacopsis quinatum*, Bombaceae) in July. (These larvae came from eggs laid by wild females in mid-June 1985, well after the rainy season began.) After the larvae pupated (in the top 1–2 cm of the soil) in late July to early August, the non-parasitized pupae were isolated one per bag in dry plastic bags and hung in a building where they were exposed to relatively ambient conditions. About 20% of these pupae eclosed in late September and October. Some wild pupae also eclosed then, as shown by the presence of second generation caterpillars feeding in *B. quinatum* trees in October–November. In mid-November, a second large cohort of wild caterpillars was collected and treated in the same manner as was the first-generation cohort. More than 40 of these second generation pupae were hung interspersed with the 35 dormant pupae of the first-generation pupae. Almost all of the pupae remained dormant until late June 1986, at which time 96% of all the pupae eclosed during a 2 weeks period. Of the other 4% one pupa remains living and apparently dormant at the time of this writing, (July) and three pupae eclosed during the dry season (at which time they would have had no future in the wild, since their host plants were leafless at that time).

Interpretation of this example is problematical because *A. armida* wild pupae in the soil at the end of the first generation may in fact all eclose rather than remain dormant as did the majority of pupae observed here. The temperature conditions of a plastic bag hanging in the wind are not the same as those deep in the soil even a few metres away. On the other hand, very few adults arrive at the lights at the time of the emergence of the second generation of *A. armida* adults (September–October), which strongly suggests that most of the wild pupae remain dormant at the end of the first generation.

Rothschildia lebeau (Saturniidae) spins a cocoon that hangs in the air in the forest understory, and therefore quasi-natural conditions are easier to simulate experimentally than they are for species that pupate in the soil. These large moths eclose at the beginning of the rainy season. They use 7–8 weeks to complete the life cycle from egg to adult. Of the thousands of pupae reared in the laboratory or collected in the wild during the first two generations of the rainy season at Santa Rosa, only one has entered pupal dormancy. The third generation occurs in October–November and pupal dormancy begins to appear. For example, in 1985, 144 siblings pupated in large screen nets in the wild in late November. All the cocoons were moved to a large outdoor screen cage where they were hung side by side. Of these, only 13% eclosed in December 1985. The remainder eclosed between 16 April and 21 June 1986 (90% in May). In a similar experiment performed 2 years before, a fourth generation of pupae was obtained from the third generation that eclosed in December. Their pupae (February) all remained dormant and their eclosion dates (at the beginning of the following rainy season) were indistinguishable from those of the third generation pupae.

Study of the degree of pupal dormancy in a multivoltine species in a seasonally dry forest is further complicated by an artifact of seasonal abundance of caterpillars. Caterpillars are most abundant in the field during the first generation, and therefore easiest to find. The large consequent samples therefore document the dormancy tendencies of the first generation. However, it may be the caterpillars at very low density in the generations occurring at the end of the rainy season that are both most likely to go into pupal dormancy and therefore most likely to contribute heavily to the pool of dry season pupae. These low density caterpillars are, however, extremely hard to find; it becomes tempting to use the degree of dormancy registered by the first generation pupae as representative of all generations. This caveat is especially important if it is a species of moth that rarely has dormant pupae in the rainy season.

(2) *Initiation of pupal dormancy*. Circumstantial evidence at Santa Rosa suggests that it is the rising temperatures associated with the oncoming dry season that are the cue for initiation of pupal dormancy in multivoltine species. However, merely being subjected to very warm weather does not automatically cause Santa Rosa moth pupae to enter dormancy. For example, during an experimental examination of the environmental cueing of pupal dormancy in *Rothschildia lebeau* (Janzen, 1984c), heating pupae to dry season temperatures (34–38°C) during the daytime in the rainy season and letting them cool back down to ambient temperatures at night did not cause them to become dormant.

(3) *Breaking dormancy*. Given that a Santa Rosa pupa is dormant, how does it perceive the presence of the season in which to eclose? In a seasonal tropical site, moths often first appear at lights at the beginning of the rainy season. It is therefore widely assumed that they use the rains as the cue for pupal eclosion. However, indirect evidence suggests that, at Santa Rosa at least, temperature and/or its changes, rather than the actual moisture brought by rainfall, cue pupal eclosion. First, for the univoltine species with pupae that remain dormant throughout the second two thirds of the wet season as well as through the following dry season (e.g., *Schausiella santarosensis* mentioned above), simply being exposed to moisture is obviously not the cue for reinitiation of development. Second, the pupae of some species are very deep in the soil as pupae (e.g., *Manduca dilucida* mentioned above) and therefore cannot be using changes in day-length as an eclosion cue. Third, there is in fact a dramatic drop in the air and soil temperature at the beginning of the rainy season (Fig. 1), a change that may occur as much as a week before really soaking rains actually arrive. Fourth, while not discussed in detail here, the dormant pupae of several Santa Rosa species (e.g., the saturniids *Rothschildia erycina* and *Copaxa moinieri*), are conspicuous in eclosing a few days after a spell of several exceptionally cool days (nocturnal lows of 17–18°C, diurnal highs of 25–28°C).

In an explicit experiment, *Rothschildia lebeau* pupae remained dormant through the Santa Rosa 1984 dry season in wet and dry plastic bags for 6 months, and eclosed from 2 weeks before to 2 weeks after the beginning of the rainy season irrespective of which type of bag they were in. However, a large sample of sibs, transplanted to a cool air-conditioned laboratory (21–24°C) in Philadelphia 2 weeks after pupation, all eclosed 1–3 weeks after their arrival. *Manduca dilucida* pupae transferred likewise to a cool laboratory behaved in a similar manner.

There is, however, a suggestion that for some species the cue to break dormancy may be more complicated than just a drop in temperature. Half of a large sample of sibling *Copaxa moinieri* (Saturniidae) was hung in dry bags in the hot conditions of the Santa Rosa dry season, and the other half was taken to Philadelphia and hung in a cool and constant temperature laboratory. Both sets of moths eclosed in April.

(4) *The biotic risks of being dormant as a pupa*. Santa Rosa is a multi-specific foraging array of potential pupal predators (e.g., ants, fungi, mice, rats, armadillos, peccaries, coatis, tinamous) and para-

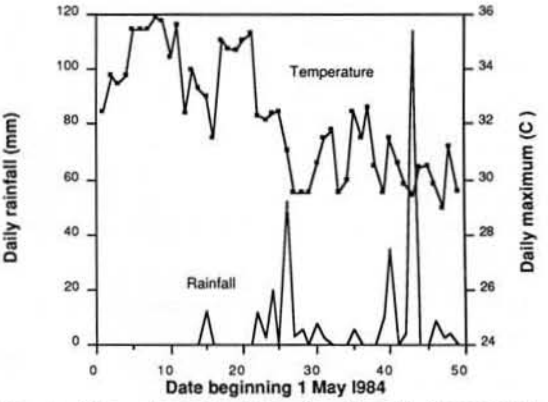

Fig. 1. The dramatic drop in diurnal (maximum) temperatures that occurs in the dry forest in Santa Rosa National Park when the rainy season begins.

sitoids (e.g., chalcidoids, ichneumonids, braconids) that generally do not die, leave or become dormant unless they run out of prey. This predation regime therefore differs significantly from that of extra-tropical winters, where many carnivores are absent, dormant or ineffectual. In short, tropical pupae do not have a winter on their side. As has been discussed by Ian Gauld (this issue), this means that the pupal resource is relatively larger for parasites and predators than is the same biomass of pupae more serenely passing an extra-tropical winter.

Pupae cannot run or fly away, and at least most of the Santa Rosa pupae appear to be highly edible to chewing predators. For example, I know of only one species of moth pupa—that of the malodorous *Dirphia avia*—that is rejected by foraging *Liomys salvini* (Heteromyidae) mice. Their primary protection appears to be: (a) in the site of pupation (*Manduca* sphingid pupae 10 cm below the soil surface are better protected than are *Xylophanes* sphingid pupae in the litter), (b) the toughness of the silk cocoon (however, a very large number of Santa Rosa moth species do not spin cocoons), (c) the toughness of the pupal wall (only relevant with respect to very small predators and parasitoids), and (d) behaviour, though the repertoire is limited (many of the large pupae in the litter make thrashing or sinuous movements when touched that are very reminiscent of the movements of a snake or snake tail).

(5) *The abiotic risks of being dormant as a pupa hiding in litter*. During the rainy season, desiccation is probably not a threat for Santa Rosa moth pupae, unless there is a severe veranillo (short dry season in the middle of the rainy season). The pupae in soil or litter are subject to 100% relative humidity at night and much of the day, and those in leaf rolls and other plant parts are also in microhabitats with very high humidity. However, as the dry season develops, the environment dries out in a very heterogeneous manner, but the pupa that is in a dry micro-site cannot move to a new one or follow a moisture gradient. This means that the prepupal larva is confronted with the difficult task of locating a site (during the homogeneously moist rainy season) that will remain moist; that is, the site selection occurs before the habitat's moisture heterogeneity is expressed. Worse, the tropical dry season differs strongly from most extra-tropical winters in being hot as well as dry. The hotter the site the more desiccating it will be for both the ambient conditions and for the pupa itself. Finally, the Santa Rosa dry season is even hotter than is the rainy season (e.g. Fig.1), and therefore intrinsically more desiccating than is the rainy season.

A pupa is not a sealed container. Sphingid and saturniid pupae at Santa Rosa may lose as much as half their body weight when passing the dry season in dry plastic bags in the laboratory; however water loss by these large pupae has not been studied in the field. Saturniid pupae contain proportionally less water than do sphingid pupae, but have thicker and heavier pupal cases than do sphingids (except for the cocoon-spinning *Rothschildia* and *Copaxa*). Small pupae, such as pyraustine pyralids, appear to die from simple desiccation if stored in the laboratory in dry bags. These observations underline the possibility that the water content of a Santa Rosa pupa may be critical to the moth's survival, and the relationship of the exact location of a pupa in the habitat may be as important in avoiding water loss in a hot dry habitat as it is in avoiding predators.

(6) *Pupa versus prepupa*. A prepupa may be able to resist some of the challenges confronting a pupa in the dry season in Santa Rosa. All species of Santa Rosa moths known to pass the dry season as prepupae do so inside a tightly spun silk cocoon (in contrast, many Santa Rosa pupae are naked or nearly so in the litter or the soil). As mentioned earlier, these cocoons are repaired if cut into—but the usefulness of this behaviour in nature is unclear; I know of no predator that would cut through a cocoon wall and then abandon the cocoon without eating the larva. The active larva in the cocoon may be able to physically avoid the ovipositor of a parasitic hymenopteran, though in fact the prepupa generally fills the space in the cocoon so thoroughly that such behavioural escape does not appear to be a very likely function of being a prepupa. I hypothesize that the potential value to being a prepupa during the dry season is that the internal immunological anti-parasitoid defenses of the larva are still fully functional.

(7) *Synchrony of pupal eclosion*. When rearing large cohorts of saturniids and sphingids under relatively ambient conditions in the laboratory at Santa Rosa, an occasional moth ecloses at a time of year when it obviously could neither find a host plant nor mate. Occasional individuals similarly out of phase with their conspecifics also appear at the lights. Such animals may have received a cue not received by the other members of the cohort, may have made a physiological error (due to a faulty genetic programme or incorrect conditioning at an earlier stage), or may be the consequence of directional selection for variation in response to a given cue. All three cases are reasonable possibilities at Santa Rosa.

The seasonality of Santa Rosa's dry forest is extremely irregular in pattern and intensity within and between years. Temperature and moisture conditions are very heterogeneous on a small as well as on a large scale. It should be virtually impossible to select for a physiological machine so perceptive and capable of evaluating cues and pseudocues for eclosion that no major errors would occur. Furthermore, there may not even be reliable indicators that a sustained period of rain is about to begin. Second, such selection would have to be extremely directional and/or in the same direction for a very long time; such directionality is not likely in the present mosaic of temperature and moisture regimes present in Costa Rican dry forest and neighbouring rainforest (which is also occupied by many of the Santa Rosa species). Third, it is very likely that the moths being discussed here (except perhaps for *S. santarosensis* and the very few other endemics, were evolutionarily invented elsewhere and have arrived simply as natural invaders (Janzen, 1985b). These colonists survive at various densities in various habitats, simply because they have such and such characteristics, not because of the degree of "success" of any particular fine-tuning evolutionary process. In this context, death of a pupa through errors vis-a-vis the abiotic environment is no different from the pupal death by predation or parasitism, or caterpillar death due to being laid on an inadequate host plant. A small to moderate number of lethal errors in pupal biology is as reasonable to expect as is losing a small to moderate number of caterpillars to predation by birds.

(III) *Undergo larval development*

Moths that survive the Santa Rosa dry season as a growing and active larval populations are almost absent during the dry season except for four very specific life styles: fruit- and seed-miners, stem-miners, case bearers, and guano- and nest-occupants. The general absence of leaf-eaters is presumably because many species of plants are deciduous and the air is dry enough to be a physiological strain on the larvae that do have leaves to eat. However, there are a very few leaf-eaters present in the early dry season. These represent the last generations of multivoltine species that have several rainy season generations and are finely forced into dormancy by the oncoming dry season (e.g., the fourth generation *Rothschildia lebeau* example mentioned earlier). I have located only one leaf-eater that breeds continually through the dry season—a social and web-forming epipaschiine pyralid (*Stericta albifasciata*) that feeds on the evergreen understory treelet *Ocotea veraguensis* (Lauraceae). Curiously, one of the few butterflies that breeds in the dry season (as well as in the wet season) in Santa Rosa, a large *Prepona* (Nymphalidae), also has larvae that feed on *O. veraguensis*.

(1) *Fruit- and seed-miners*. The larvae of one or more species of fruit- and seed-miners can be found in all months of the year, and almost all of them are pyraustine, phycitine and chrysaugine Pyralidae. Each species has a distinctive larval season associated with the timing of the presence of larval food. More kinds and bulk of fruits and seeds are available in the dry season than in the wet (e.g. Janzen, 1967), and many more species go through larval development in the dry season than in the wet. Fruits and seeds are also a more hospitable environment for mining Lepidoptera larvae in the dry season than in the wet. In the wet season, exit and entrance holes allow rain to enter, thereby both rendering the damaged material a soggy mess and maximizing the rate of growth of decomposers that are potentially detrimental to the larva.

Fruits and seeds that are suitable for larval development are not available during all months of the dry season. As nearly as I can determine from captures at lights, the adults of these species are free-flying in the habitat when the relevant fruits and seeds are absent. However, they probably spend most of their time sequestered in locally humid cracks and crannies (or visiting flowers or other moisture sources). However, irrespective of what time of year larval foods are available, there are many months during the year when there appear to be no larval foods for the Santa Rosa fruit- or seed-mining pyralids. If a species has larvae that eat fruits or seeds that are available in the dry season, then the season to be endured is the rainy season (as is also the case with the seed predator bruchids and weevils in the same habitat; Janzen, 1973).

While I do not dwell on this problem in this paper, these moths pass the rainy season in three ways. Some, like the phycitine *Ectomyelois muricis* (whose larvae feed in the large fruits of *Hymenaea courbaril* from about December through April; Janzen, 1983a) are active adults in the foliage and occasionally appear at lights in the rainy season. Others, like the phycitine that mines in *Canavalia maritima* (Leguminosae) fruits, spin a tough cocoon in the litter and then remain in the cocoon for many months as an active prepupa before finally pupating and emerging almost a year later. Finally, there are phycitines like *Hypsipyla grandella*, which has a generation in the nearly mature fruits of *Cedrela odorata* and *Swietenia macrophylla* during the mid-dry season and then ecloses; the free-flying adults then wait until the first shoots of these two plants appear at the beginning of the rainy season and lay eggs that immediately generate shoot miners. After at least two generations as shoot miners, they are then again able to wait as adults until the fruits approach maturity in the early-mid dry season, and at which time the cycle starts over again.

I do not yet know what proportion of the tens of species of Santa Rosa fruit- and seed-mining pyralidae belong in each of the above three categories, but there are numerous species in each. Additionally, in at least one case besides that of *Hypsipyla*, a phycitine pyralid has two species of fruit and seed hosts and uses different ones at different times of the dry season.

(2) *Stem miners*. The larvae of Cossidae are conspicuously present as miners in living and moribund woody stems and trunks throughout the year in Santa Rosa. There is a conspicuous peak of appearance of species and individuals of adult Cossidae at the lights in the first 3 months of the dry season (December–February). Cossids do not feed as adults, are apparently short-lived, and apparently do not migrate. It is therefore likely that Cossidae display an aggregate peak of oviposition in the first three months of the dry season. This is the windiest time of year and the time of year of greatest wind damage to living branches and entire trees (by windthrow). If cossid larvae use cracks and wounds in surfaces to gain access to tree trunks, and if rain in their initial burrows is detrimental, then the first half of the dry season may well be the most favourable time to initiate mines. In sum, cossid larvae survive the dry

season by being distant from it in cool and humid tunnels and the adults are seasonally active in such a manner as to suggest that the first third of the dry season (cooler and more moist than is the remainder of the dry season) is the time of year most favourable to them.

There is one species of bark/cambium-eating larva in the Tineidae that is also conspicuously present on the boles of forest understory saplings throughout the dry season. It has a very tough and seemingly desiccation-resistant cuticle and spends much of its time in holes and crevices in the sapling stem. It spins a silk and frass covering over its feeding and resting area. This covering probably maintains high humidity in the small space below it (from the moisture in the bark where the larva is feeding).

(3) *Case bearers*. There are only three species of Psychidae known to occur at Santa Rosa. All three have been found as larvae in their cases in the dry as well as in the wet season, but they appear to feed in the dry season only when the particular plant they are on is still bearing leaves. When it leafs out, the larvae begin feeding again. The same may be said for two of the approximately 10 species of Mimallonidae in Santa Rosa.

(4) *Guano and nest occupants*. Guano from bats and porcupines, *Coendu mexicanum*, in the bases of hollow trees and caves in Santa Rosa are extensively tunneled in and fed upon by the larvae of Tineidae during the dry season. During the rainy season, many guano deposits are either washed away or become soggy fermenting sludge. As with fruit- and seed-miners, the rainy season seems to be the harsh time of year for guano-feeding Lepidoptera larvae. Presumed nest occupants, such as the larvae of the mouse moth *Ptilopsaltis santarosae* (Tineidae) (Davis *et al.* 1986), are probably less susceptible to seasonal change in climate and thus more cossid-like in their relationship to weather. However, mouse moth adults are encountered riding on the backs of *Liomys salvini* mice (Fig. 1 in Davis *et al.*, 1986) in all months of the year at Santa Rosa.

(IV) *Remain in Santa Rosa as a potentially active adult*

Moths in a warm inimicable season have the evolutionary option of being potentially active adults rather than dormant immature stages. However, this option is not equally available to all life forms. Many moth families are made up of non-feeding adults and these adults have only 5–10 day adult life spans (e.g., Saturniidae, Megalopygidae, Mimallonidae, Apatelodidae, Limacodidae, Lymantriidae, Lasiocampidae, Cossidae). All the species that I have reared to date in these families in Santa Rosa, except for the *Hylesia lineata* mentioned earlier, pass the dry season as dormant pupae. However, the array of species of moths that may live for weeks to months as adults contains many species that have pupae that remain dormant through only part of the dry season and then eclose to an adult form. The adult can both avoid predators and desiccation through appropriate movements.

While as yet only preliminarily documented, the species richness (and perhaps numbers) of adult moths in the Park during most or all of the dry season is very great. However, they are not species that have feeding larval forms during the dry season. Most of them do not even oviposit on odd individuals of their host plants that happen to have leaves during the dry season. These moths are very difficult to census and are also subject to a biological confusion based on differential arrival at lights in the wet and dry seasons.

Potentially active moth adults are difficult to census during the dry season because they often do not arrive at lights. That they are however present in the habitat is shown by three things:

(1) Single adults are often flushed from crevices, undersides of leaves, the litter, tree bark and other semi-protected sites in the forest in the daytime in the dry season. Almost all of these moths are in the family Noctuidae, and many of them are species that visit flowers or rotting fruits.

(2) A small number of individuals do arrive at the lights each night. The species richness among these arrivals is very high; collecting over many nights accumulates hundreds of species. Except for the cossids, adults of virtually all of these species have functional mouthparts.

(3) If there is rain or humid/cloudy spell in the mid-dry season (as occurred in March 1984), an enormous number of adults of these species appears immediately at the lights. For example, if the rain is at 4–5 pm and the night is calm, the lights are beseiged with moths immediately after sunset. These moths certainly did not emerge from pupae or migrate into the site in the 1–2 hr since the rain fell. Additionally, they do not continue to appear at the lights as the dry season continues.

I interpret these observations as follows. Most of these adult moths are in reproductive dormancy waiting for the dry season to pass. They spend much of their time sitting in secluded places where their rate of water loss is minimal during the dry daylight hours (and where they are the least likely to be flushed by a foraging predator, thereby exposing them to a potentially desiccating flight through very dry air). Even at night they fly only if there is a nectar or other food source in the vicinity (when they fly they are exposed to predation by bats and may lose a good diurnal resting site). They are not involved in mating very much if at all, and thus do not fly much at night in search of females; this should greatly diminish the number of adults to arrive at the lights (cf. Janzen, 1984a). Likewise, very few females will pass near enough to the lights to arrive at them, since the females are not out searching for oviposition sources. However, when rain occurs, many species respond as though the rainy season has begun and initiate the search for habitats, mates and oviposition sites that characterizes adult moth behaviour at the beginning of the rainy season. These moths then appear at the lights in large numbers.

The biological confusion lies in the question of exactly where the adults that are active in the dry season come from. There are four major potential sources (for the moment I will ignore migrants):

(1) The moths could have emerged during the final months of the rainy season and are simply waiting throughout the dry season, as is normal behaviour

for that species. In such a situation, the adult population would be at its highest dry season density at the beginning of the dry season, and then gradually decline until the beginning of the rainy season.

(2) The moths could be aging members of a population, gradually dying at a rate that is dependent on predators, moistness of the particular year, food availability, etc. The remainder of the population would be migrants in some other habitat or dormant pupae. That is to say, the active adults are senescing individuals and their presence is not likely to be the direct result of selection for this phenology. Their relative importance in the overall biology of a species of moth would decline with the length and severity of the dry season.

(3) The moths could be emergence errors (or necessities). In other words, the population starts the dry season as pupae, but a few individuals find themselves in too dry a site or not receiving the appropriate cues to persist as a dormant pupa (or they receive a false eclosion cue). They then emerge and attempt to survive the remainder of the dry season as adults. For example, in a sample of 37 pupae of *Hemicephalis agenoria* Druce (Noctuidae) from its single generation on *Cordia panamensis* (Boraginaceae) in the first 6 weeks of the rainy season in 1984, one eclosed in December 1984, two eclosed in March of 1985, and 34 eclosed between late April and early June of 1985. In populations such as these, the density of adult moths during the dry season could do anything from jiggle up and down to decline or increase, depending on the year or the particular species of moth. The females of such newly emerging moths may pheromonally call males immediately after eclosion, as they do in the rainy season, and therefore be a large part of the cause of males arriving at lights during the dry season.

(4) The moths could spend part of the dry season as dormant pupae and then the adults eclose at some internally or externally programmed time in the dry season (i.e., at some fixed interval or cue before the rainy season begins). The third category of moths mentioned above may blend directly into this fourth category, and/or represent the evolutionary forerunners to it. As the rainy season approaches, this fourth category appears to make up a progressively larger fraction of the species that arrive at the lights up to the night of the first rains. However, such moths are also very difficult to distinguish from species that are migrating into the Park near the beginning of the rainy season. There is one subset of this category, however, that is not difficult to recognize as anticipating the beginning of the rainy season. The non-feeding and non-migratory species that eclose before the first heavy rains, such as the rust-coloured morphs of *Rothschildia lebeau* (Janzen, 1984c), are unambiguously betting that there will in fact be a rainy season and that it is being heralded by the changes in temperature (Fig. 1) that predate the really soaking rains and major leafing out of host plants.

In sum, a moth that is perched on a leafless branch in Santa Rosa in late March, or comes to a light that night, may well be an error, a senescent moth, a normal long-distance runner, or conspicuously anticipating the beginning of the rainy season. The latter is not quite as outrageous as it may seem, since there can be many nectar sources during the last month of the dry season and some trees anticipate the rains by putting out new foliage as much as a month before the rains arrive.

(V) *Migrate out of Santa Rosa*

The moth fauna of Santa Rosa National Park is not a self-contained ecological entity. Many species that pass at least one larval generation in Santa Rosa are elsewhere during all or part of the dry season, and some species are elsewhere for part of the rainy season as well. There are at least two distinct processes that lead to this temporal distribution pattern. First, there are populations that are extinguished from the Park by an inclement season, and then are re-established by wanderers or invaders in search of host plants in a subsequent breeding season. This process occurs at Santa Rosa, but it is not the subject of the current essay because it only marginally fits under the rubric of "a way to pass the dry season". Furthermore, it should probably not be termed "migration".

Second, there are the moth species for which many or all of the members fly away from Santa Rosa at specific time(s) of year. At a later and usually specific time, members of that species then return and have one or more further generations in the Park. Here I call these migrant species and assume that the behaviour is one that has either evolved specifically with respect to the seasonality of dry forest resources, or one that evolved in response to some other fluctuating resource and now functions in a seasonal habitat. At Santa Rosa, sphingid moths provide the most conspicuous examples of migration by moths but noctuids appear to do it as well. All the species that appear to be migrants can and do feed as adults.

A representative migrant sphingid has the following life history at Santa Rosa. From a few days before until a few days after the beginning of the rainy season in late April to mid-May, the adults fly into the Park. They oviposit for a few weeks on their one or few host plant species and die. The larvae take a species-specific period of two to four weeks to develop, and then pupate. The adult ecloses 2–6 weeks later. In many species, most of these adults then leave the Park, but a few remain behind to attempt another generation in the middle and (even) late part of the rainy season. In a few species, many members appear to stay for a second generation. The adult moths of all the presumed migrants are then gone during the 6 month dry season.

How do I know that the adults eclose at the end of the first generation rather than that some or all of them remain as dormant pupae in the litter or soil? First, the pupae in captivity (from wild-caught caterpillars in May–June) never remain dormant, irrespective of whether they are in dry or moist soil, or subjected to high or low temperatures (but, as mentioned above, it is still theoretically possible that certain ambient conditions would induce pupal dormancy). There is one exception. In laboratory rearings of wild-caught *Xylophanes turbata* caterpillars, about 10% of the pupae become dormant at the end of the first generation in late June to early July; these then wait through the remainder of the rainy season and all of the dry season, and then eclose in response to the drop in temperature that occurs with the first rains. The remaining 90% emerge and apparently migrate out of the Park within 3 to 4 weeks after pupating; there is no second rainy season generation on their conspicuous host plants (*Hamelia patens* and *Psychotria microdon*, Rubiaceae). This moth is presently known only from the dry Guanacaste lowlands and the immediately adjacent evergreen forest. The pupae of *X. turbata* have noticeably thicker pupal cuticle than do those of the other nine species of *Xylophanes* that breed in Santa Rosa, and it seems reasonable to view it as a dry forest specialist.

How do I know that the adult sphingids actually leave the Park? First, while many adults eclose from the first generation in July and August, larvae of the presumed migrant species are almost non-existent in the Park from August through the remainder of the rainy season (and the dry season). Second, wild adults are common in the forest during the period of adult emergence in the laboratory (at some species-specific time between late July and August). The adults come to lights and are common at flowers, in addition to being encountered resting on the foliage. Then all or most of them simply disappear. During an outbreak, such as was recorded with the small diurnal sphingid *Aellopos titan* in 1983 (Janzen, 1985a), this abundance and subsequent disappearance of adults is especially conspicuous. Third, sphingids probably do not live long enough as adults for the individuals that apparently disappear from the Park in July–August to be the same individuals that oviposit in the Park in the following May. Therefore, they have to have had a second or more generation elsewhere. Fourth, they are all species that can be caught at wetter sites in Costa Rica during other parts of the year.

Where do the sphingids go when they leave the Park? Several lines of evidence suggest that they go to the wetter or "rainforest" parts of Costa Rica. First, there is no reason for them to go to other dry forest to pass the remainder of the year (and there is no collection data to suggest that they do, although most of the Costa Rican dry forest has now been sufficiently destroyed that the terrain lacks vegetation that would be of use to them). Second, all the presumed migrant species in Santa Rosa occur in the rainforested parts of Costa Rica during the second half of the Santa Rosa rainy season and during the Santa Rosa dry season (they are also present at the other times of year). Third, these same species are commonly captured at lights placed in the passes in the mountain chains separating the dry from the rain forest (e.g., Janzen, 1984a); these passes (and collection sites sometimes well above them) are at elevations hundreds to thousands of metres higher than where the larval host plants of these species occur. It is difficult to avoid the inference that these moths are flying through the passes from the dry forest to the rainforest (and back). Fourth, there is strong periodicity in the appearance of these species of sphingids at lights on the rainforest side of Costa Rica; while this may be generated by *in situ* biological processes, it could also be generated by the arrival and departure of migrants.

Do they reproduce while they are gone from Santa Rosa? Circumstantial evidence suggests that they do. First, as mentioned above, there is no evidence to suggest that sphingids, long-lived as they are, will live as active non-reproductive adults for the 10 months between breeding periods in the Park. Second, the specimens that arrive at the Park at the beginning of the rainy season are often very fresh in appearance rather than having the worn wings of older moths; this implies that they are newly emerged individuals from the most recent rainforest generation rather than original moths that left the Park 10 months earlier. Third, the rainforest contains either the same host plant species or genera that are their host plants in the Park; there are sphingid larvae of the appropriate species on these hosts during the time that the moths are absent from Santa Rosa. Fourth, in at least one case (*Perigonia lusca*), the moths that appear with the beginning of the rains are larger than are those that left the Park in the middle of the previous rainy season (Janzen, 1984a), and therefore must have passed a generation outside of the Park.

DISCUSSION

The biology of seasonality in tropical insects (e.g., McElravy *et al.*, 1982; Wolda, 1980, 1982, 1983, 1984; Wolda and Broadhead, 1985; Wolda and Denlinger, 1984; Wolda and Fisk 1981; Wolda and Galindo, 1981; Wolda and Flowers, 1985; Jacquemard, 1976; Cantello, 1974; Denlinger, 1974, 1978, 1979, 1980, 1986; Denlinger and Shukla, 1984; Dingle and Baldwin, 1983; Jones and Rienks, 1987; Jones *et al.*, 1985; Monteith, 1982; DeVries, 1983; Owen and Chanter, 1972; Masaki, 1980; Tauber *et al.*, 1986; Janzen, 1973, 1976, 1979, 1983b; Morton, 1977) is a subject very much in its infancy. However, even at this early stage of exploration it is obviously very rich in pattern, far richer than is the case in the climatically monotonous extra-tropical habitats. Tropical habitats have nearly infinite potential for generating complex interactions between biological and climatic heterogeneity. Furthermore, the biological diversity generated by these interactions yields yet more biologically diverse substrate for further interaction with the climate in one direction, and other organisms in another direction.

Documenting tropical insect seasonality and experimentally dissecting its causes has very great potential in both the preservation and manipulation of tropical insects. It is already clear that one cannot ask merely about the biological consequences of minimal sizes of conservation areas, of irrigation, of El Niño, of a dry season, etc. The answers will depend on what species, life forms, trophic levels, etc. of insects are focal, and under what environmental regime a perturbation occurs. The answers will even depend on whether the focal insects are transient or remnant populations, on their way to extinction or another site (Janzen, 1986b), or breeding populations.

Santa Rosa's tropical dry forest moths do not merely turn on their reproduction when the rains come, run for several generations, and then turn off when the dry season comes. Such a pattern might well be possible if the caterpillar had only its host plants and the weather to deal with. There is, for example, no suggestion that the defensive chemistry of the foliage of dry forest trees changes as the rainy season progresses (e.g., Janzen and Waterman, 1984). If weather were the only challenge during the dry season, moths would simply pass the dry season by hiding in a very water-resistant pupal cuticle or cocoon. Furthermore, there are even a number of species of evergreen trees. If they fed on evergreen species, they could continue to do that until the water loss through desiccation became too great to be made up for by the high water content of the food.

It appears to me that the carnivores (predators and parasitoids) are the primary driving force for complicating what might otherwise be a simple seasonal on-off system. It is clear that a dormant pupa is at extreme risk from searching carnivores throughout the dry season (as well as during the rainy season); tropical carnivores do not stop searching until they run out of food. I strongly suspect that it is also the carnivores that lead to exit of migrant moths from the Park in the middle of the rainy season, a time when there is ample food and an excellent climate for their larvae. The ecological process is as follows. Throughout the dry season, ordinary mortality factors are acting on the carnivores. They should be at their lowest density at the beginning of the rainy season. After one generation of larvae and pupae on which to develop (May–June), they should be at their annually highest level. The "smart" moth will either leave the Park to have a generation elsewhere in wetter forest, remain as a well-protected dormant pupa (or prepupa), or be an active adult in some kind of reproductive dormancy. However, the rainforest is also relatively unfriendly to caterpillars. I suspect that if the migrant moths had to maintain their populations only with the survivors of successive rainforest generations, they might well be extinguished. On the other hand, the population gets a major recruitment input each year from the dry forest at the end of the first generation. In other words, the generation of the migrants by the dry forest might well be critical for survival of the population as a whole rather than merely represent an annual period of high density.

The seasonal biology of tropical moths is extremely poorly known. Gaining knowledge about them is more than a laboratory exercise in subjecting them to various physical conditions. To complicate things even further, tropical wildlands are seriously modified in two ways that obscures moth seasonal biology. First, many are embedded in large expanses of secondary succession and agricultural lands; these lands provide both biological and physical seasonal advantages to certain moths and detriments to others. Second, the seasonal movements of moths are certainly going to be affected by the destruction of the wildlands to which they traditionally migrated. The future looks very grim for the serious study of wildland moths in any context approximating the one in which they evolved or have spent much of their ecological lifetime.

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