

OXFORD SURVEYS IN EVOLUTIONARY BIOLOGY

Volume 1 : 1984

Two ways to be a tropical big moth:
Santa Rosa saturniids and sphingids

by

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The world has two species-rich families of big-bodied moths: Saturniidae and Sphingidae (Figs. 1–4). In the New World they co-occur from Canada to Patagonia, from sea level to the upper limits of vegetation, from extra-tropical deserts to the wettest tropical forests. The species-specific live body weights (e.g., Tables 1–2) occupy about the same ranges (0.1–7.0 g) but saturniids and sphingids represent two quite different ways of being a large moth. Using the saturniid and sphingid faunas of a small mosaic of dry lowland tropical habitats – 10,800 ha Santa Rosa National Park in northwestern Costa Rica – I propose and discuss answers to three conspicuous eco-evolutionary questions about their natural histories. My eventual goal is to understand the selective pressures and ecological processes that have made Santa Rosa saturniids and sphingids what they are. I fully recognize that this understanding will eventually require study of the Santa Rosa species in the other parts of their broad ranges. However, I use and discuss this local fauna because it is the one that I know the best. I use a local fauna because many of the traits discussed must be first understood in their local adaptive sense before they can be viewed in aggregate over a species' range. I restrict myself to only three questions because this is not a book.

1. Why do saturniids go to lights differently than do sphingids?
2. Why do saturniid wings differ strikingly in shape between the sexes and among species, while sphingid wings are monotonously similar in shape?
3. Why do saturniid caterpillars feed on more and different families of plants, but on fewer plant life forms, than do sphingid caterpillars?

Before embarking on the details of these questions, I offer a brief caricature of these taxonomically well-known moths (Ferguson 1972, Hodges 1971, Rothschild and Jordan 1903, Lemaire 1974, 1978, 1980, 1985, Michener 1949, 1952). While long of interest to caterpillar fanciers (e.g., Gardiner 1982, Collins and Weast 1961, Moss 1912, 1920) and often the subjects of physiological and ethological experiments, saturniids and sphingids have generally been neglected by field ecologists and evolutionary biologists (some exceptions are, Saturniidae: Blest 1960, 1963, Brown 1972, Capinera 1980, Capinera *et al.* 1980, Farge 1983, Cryan and Dirig 1977, Hogue *et al.* 1960, 1965, Janzen 1984a, 1984b, 1984c, Wangberg 1983, Marsh 1937, Peigler 1975, 1976b, 1981, 1983, Smith and Turner 1979, Quezada 1973, White 1972, Carolin and Knopf 1968, Lawson *et al.* 1982, Beutelspacher 1978, Vuattoux 1981, Crocomo and Parra 1979, van den Berg 1974a, 1974b, van den Berg and van den Berg 1974, van den Berg *et al.* 1973, Waldbauer and Sternburg 1967, 1973, 1979, 1982a, Waldbauer *et al.* 1984, Sternburg and Waldbauer 1969, 1978, Scarborough *et al.* 1974,

Sternburg *et al.* 1981, Janzen and Waterman 1984, Scriber 1977, 1978, Rivnay 1970, Rivnay and Sobrio 1967; Sphingidae: Bullock and Pescador 1983, Fleming 1970, Gregory 1963, Rivnay and Yathom 1967, Beutelspacher 1978, Young 1972, Janzen and Waterman 1984, Janzen 1984b, Grant 1937, Laroca and Mielke 1975, Casey 1976, Schneider 1973, Stewart 1969, 1975, Thurston and Prachuabmoh 1971, Owen 1969, 1972, Vuattoux 1978, Giles 1968, Haber 1983a, 1983b, Haber and Frankie 1984, Wolda 1980, Dillon *et al.* 1983).

The style of this essay departs from convention in that much of it is based on data from an unpublished study still in progress. Rather than decorate every other sentence with 'Janzen, unpublished' I assume that the reader will recognize the source. Likewise unconventionally, I dwell on the implications of traits evident in the field and what they may mean in big moth biology rather than on documenting their means and variances. I am willing to relax my scrutiny of individual trees in order to keep the forest in view. My generalizations are, however, intended to apply only to the Santa Rosa saturniid and sphingid faunas, and do occasionally deviate from those for these moths in other regions.

The saturniid nomenclature followed here is that used by C. Lemaire, the most recent reviser of the family (Lemaire 1974, 1978, 1980, 1985). I depart from using *Sphingicampa* and *Oiticicia* as was used in my guide to the saturniids of the Park (Janzen 1982), in deference to *Syssphinx* and *Othorene* (Lemaire 1985). Sphingid names are those used by Hodges (1981) and Haber (1983a). All species of saturniids and sphingids mentioned here by name are easily identified at Santa Rosa, and I am deeply indebted to C. Lemaire, J. Cadiou, R. Hodges and W. Haber for confirming my field determinations.

Saturniid caricature

Adult Santa Rosa saturniids (Figs. 1–2) are medium-weight to very heavy moths (Table 1). All but one of the 30 species that breed in the Park (Janzen 1982), *Schausiella santarosensis* (Lemaire 1982), range over many tens of degrees of latitude (C. Lemaire, personal communication); the most widespread is the imperial moth, *Eacles imperialis* (Fig. 1.7–1.8; Canada to Argentina (Lemaire 1985)). The adults fly during at least part of the night and spend the day hanging motionless and cryptic in the vegetation; their diurnal goal is to avoid desiccation and discovery by carnivores. Some make mimetic or aposematic displays after being discovered (e.g., *Citheronia*, *Arsenura armida*, *Automeris*, *Hylesia*, *Dirphia*, *Ptiloscola*, *Periphoba*, *Molippa*). Saturniid adults have only rudimentary mouthparts and apparently do not feed; they harvest all of their water and nutrient resources while they are caterpillars. Immediately after eclosing from the pupa and leaving the cocoon or underground pupation chamber, the adult hangs from vegetation and expands its wings. Without having flown, the female pheromonally calls males on the night of eclosion (all non-hemileucines and *Periphoba*) or in the night immediately following an

afternoon eclosion from the pupa (*Automeris*, *Dirphia*, *Hylesia*). She often mates with the first male to arrive (but see Brown 1972) and mates only once. She lays 40 per cent or more of her eggs during the next night (see Rau and Rau 1913, Miller 1978, Miller and Cooper 1977, for extra-tropical examples) and within two to eight more days she lays the remainder of her eggs and dies. She lays her eggs irrespective of whether she has located larval host plants. The male flies shortly after dusk, and then again later in the night when seeking calling females (except for the males of *Dirphia avia* and *Adeloneivaia isara*, whose females call shortly after dusk). He may stay in copula for less than an hour (*Dirphia*, *Automeris*) or until the afternoon of the following day. He is capable of mating on successive nights and the successively mated females lay fertile eggs. He lives about the same number of nights as does the female (five to 12). Death, in both sexes, is associated with attacks by predators, wing wear, weight loss (e.g., Waldbauer *et al.* 1984), and body-water loss; however, death occurs after five to 12 days irrespective of environmental events. Wild females customarily weigh two to four times as much as do conspecific males at the time of eclosion (Table 2) and usually produce 200–500 large eggs weighing 2 mg (e.g., *Adeloneivaia isara*, *Automeris rubrescens*) to 11 mg each (e.g., *Eacles imperialis*). For a more familiar reference point, cecropia moth (*Hyalophora cecropia*) eggs weigh 4.7 mg each (Schroeder 1972). The female's initial egg load usually constitutes more than half her initial body weight, but as she oviposits her weight approaches that of the male (Table 1, compare weights of moths at lights with weights at eclosion).

The eggs hatch in six to 15 days and except for *Hylesia lineata* (Janzen 1984a), are not the stage that passes the severe five-month rainless season at Santa Rosa. Larvae feed for four to five weeks (non-hemileucines) or six to 10 weeks (hemileucines). The pupal stage lasts about three weeks or else pupae become dormant during the long dry season. Caterpillars of all species feed on adult (and rarely juvenile) dicot woody plants (Table 3); all feed externally on the leaf blades of mature foliage, and, except for certain hemileucines and *Copaxa moinieri* and *Syssphinx mexicana*, all are found primarily in the crowns of large trees. Over 50 per cent have Leguminosae among their host plants. More than half of the species at Santa Rosa have two or more larval host plants that are in different families (Table 3). While all rest on the foliage, some species also rest in silk leaf-nests (*Hylesia lineata*, Janzen 1984a) or away from the foliage (e.g., *Dirphia avia*, *Citheronia lobesis*). They occasionally defoliate their host plants (e.g., Janzen 1981, 1984a). Saturniid caterpillars are conspicuously subject to vertebrate and invertebrate predation, parasitoids, diseases, inclement weather, and intra-specific competition (direct during defoliation events, diffuse all the time through sharing carnivores). The larvae vary strongly among species as to whether they are cryptic, aposematic and/or mimetic of urticators; at least 40 per cent urticate, and other 30 per cent are mimics of urticators. Larval colour polymorphism is rare within an instar and usually produced by crowding or shading (e.g. Hintze-Podufal 1977). The last larval instar leaves the host plant to spin a cocoon or burrow into litter or soil to form a pupation chamber. Larval and pupal duration are

Table 1

Live weights (g) of the Santa Rosa breeding saturniids taken at lights (therefore of mixed ages) and newly eclosed (wild reared only). The newly eclosed weight is that of a representative maximum sized individual.

	Males				Females			
	\bar{X}	At lights s.d.	n	New eclose	\bar{X}	At lights s.d.	n	New eclose
Arsenurinae								
<i>Arsenura armida</i>	.83	.17	10	1.2	1.28	.46	4	3.7
<i>Caio championi</i>	.91	.26	10	1.5	2.15	.84	10	4.2
<i>Copiopteryx semiramis</i>	.69	.17	10	NA	.55	.20	2	NA
<i>Dysdaemonia boreas</i>	.90	.25	10	1.4	1.61	.51	3	3.0
<i>Titaea tamerlan</i>	.88	.25	10	1.3	2.13	.70	10	4.0
Ceratocampinae								
<i>Adeloneivaia isara</i>	.25	.06	10	.3	.46	.13	10	.6
<i>Citheronia bellavista</i>	.92	.23	10	1.4	.91	.12	2	3.3
<i>Citheronia lobesis</i>	.93	.14	10	1.3	1.19	.52	2	3.3
<i>Eacles imperialis</i>	1.30	.27	10	1.6	2.38	.91	10	7.1
<i>Othorene purpurascens</i>	.80	.15	10	1.0	1.77	.41	6	2.9
<i>Othorene verana</i>	.74	.14	10	.9	1.92	.55	7	3.0
<i>Ptiloscola dargei</i>	.34	.08	10	.4	.52	.19	10	1.3
<i>Schausiella santarosensis</i>	.77	.13	10	1.0	1.64	.57	10	2.8
<i>Syssphinx colla</i>	.85	.19	10	1.1	1.20	.49	4	2.8
<i>Syssphinx mexicana</i>	.63	.16	10	.9	1.15	.41	10	3.4
<i>Syssphinx molina</i>	.80	.33	10	1.3	1.82	.80	10	3.8
<i>Syssphinx quadrilineata</i>	.59	.13	10	.8	.99	.27	9	2.3

Hemileucinae								
<i>Automeris io</i>	.25	.05	10	.3	.82	.19	6	1.9
<i>Automeris metzli</i>	.89	.15	10	1.2	2.01	1.01	3	4.4
<i>Automeris rubrescens</i>	.38	.09	10	.5	.94	.42	10	3.0
<i>Automeris zugana</i>	.30	.06	10	.3	.66	.17	10	1.5
<i>Automeris zurobara</i>	.32	.08	10	.4	NA			2.8
<i>Dirphia avia</i>	.64	.15	10	.9	1.81	.60	10	3.5
<i>Hylesia dalina</i>	.09	.02	10	.1	.18	.10	10	0.4
<i>Hylesia lineata</i>	.10	.01	10	.1	.52	.22	10	0.6
<i>Molippa nibasa</i>	.29	.03	10	.3	.69	.06	4	1.6
<i>Periphoba arcae</i>	.58	.16	10	.8	1.45	.70	10	3.7
Saturniinae								
<i>Copaxa moinieri</i>	.30	.10	10	.4	.44	.30	4	2.0
<i>Rothschildia erycina</i>	.39	.08	10	.5	.69	.12	5	1.8
<i>Rothschildia lebeau</i>	.49	.12	10	.9	1.53	.37	10	3.1
Range	.09-1.30			.1-1.6		.18-2.38		.6-7.1

Table 2

Live weights (g) of the Santa Rosa sphingids taken at lights. Breeding species unless marked with an asterisk.

	Males			Females		
	\bar{X}	s.d.	n	\bar{X}	s.d.	n
<i>Aellopos clavipes</i>	.25		1			
<i>Aellopos fadus</i>	.62	.08	2			
<i>Aellopos titan</i>	.57	.21	3	.50		
<i>Agrius cingulatus</i>	1.42	.34	10	1.61	.39	7
<i>Aleuron carinata</i>						
* <i>Aleuron chloroptera</i>				.81		1
<i>Aleuron iphis</i>	.30		1			
<i>Ampllypterus gannascus</i>	.59	.07	10	1.13	.25	9
<i>Ampllypterus ypsilon</i>	.85	.13	10	1.36	.25	2
<i>Callionima falcifera</i>	.53	.04	10	.92	.15	10
<i>Cautethia spuria</i>	.17	.02	10	.35	.09	2
<i>Cautethia yucatanana</i>	.14	.03	10	.39		1
<i>Cocytius antaeus</i>	3.02	.53	8	4.58	.94	3
<i>Cocytius duponchel</i>	2.35	.27	10	3.21	.83	6
<i>Cocytius lucifer</i>	2.79	.43	7	4.00		1
* <i>Dalbogene igualana</i>						
* <i>Enyo gorgon</i>				.81		1
<i>Enyo lugubris</i>	1.14	.15	6	1.11	.15	5
<i>Enyo ocypete</i>	.57	.07	10	.69	.15	10
* <i>Erinnyis alope</i>	1.56	.30	3	1.29		1
<i>Erinnyis crameri</i>	.81	.21	10	1.36	.22	7
<i>Erinnyis domingonus</i>	.38		1	.54		1
<i>Erinnyis ello</i>	1.23	.35	10	1.33	.27	10
<i>Erinnyis lassauxii</i>	1.10	.25	10	2.04		1
<i>Erinnyis obscura</i>	.39	.09	10	.52	.10	7
<i>Erinnyis oenotrus</i>	.94	.11	10	1.11	.20	10
<i>Erinnyis yucatanana</i>	1.12		1			
<i>Eumorpha anchemola</i>	3.28	.32	6	4.41		1
* <i>Eumorpha fasciata</i>						
<i>Eumorpha labruscae</i>	2.59	.66	4			
<i>Eumorpha satellitia</i>	1.59	.28	10	2.31	.67	10
* <i>Eumorpha triangulum</i>	2.12		1			
<i>Eumorpha vitis</i>	1.41	.19	10	1.65	.06	2
<i>Eupyrhroglossum sagra</i>	.49	.04	10	.66	.26	2
<i>Hemeroplanes triptolemus</i>	.90	.16	10	2.16		1
* <i>Hyles lineata</i>	.45		1	1.00		1
<i>Isognathus rimosus</i>	.93	.08	10	1.68	.36	10
<i>Madoryx oiclus</i>	.98	.21	10	1.99	.30	10
* <i>Madoryx pluto</i>	1.35	.23	2			
* <i>Madoryx bubastus</i>						
<i>Manduca barnesi</i>	1.42	.30	10	2.13	.40	10

<i>Manduca corallina</i>	1.32	.08	10	1.74	.51	10
<i>Manduca dilucida</i>	.65	.07	10	.91	.23	10
<i>Manduca florestan</i>	1.16	.17	10	1.99	.41	10
<i>Manduca lanuginosa</i>	.80	.12	10	1.46	.32	10
<i>Manduca lefeburei</i>	.76	.07	10	1.02	.10	10
<i>Manduca muscosa</i>	1.08	.37	10	1.58	.24	5
<i>Manduca occulta</i>	.99	.12	10	1.48	.39	7
* <i>Manduca ochus</i>	1.55		1			
<i>Manduca rustica</i>	2.74	.53	10	3.31	.85	10
<i>Manduca sexta</i>	1.33	.23	9	1.87	.51	4
* <i>Manduca hannibal</i>						
* <i>Manduca</i> sp.						
<i>Neococytius cluentis</i>						
<i>Nyceryx coffeae</i>	.73	.08	10	.95	.14	6
<i>Nyceryx riscus</i>	.39	.07	10	.64	.17	3
<i>Pachygonia drucei</i>						
<i>Pachylia ficus</i>	2.12	.34	10	2.91	1.23	4
<i>Pachylia syces</i>	2.55	.39	3	2.73		1
<i>Pachylioides resumens</i>	.95	.14	10	1.42	.14	9
<i>Perigonia lusca</i>	.57	.17	10	.68	.13	10
<i>Phryxus caicus</i>	.38		1			
<i>Protambulyx strigilis</i>	.74	.11	10	1.11	.41	10
* <i>Protambulyx xanthus</i>						
<i>Pseudosphinx tetrio</i>	2.30	.37	5			
<i>Sphinx merops</i>	.79	.12	10	1.32	.13	2
* <i>Unzela japyx</i>						
<i>Unzela pronoe</i>						
<i>Xylophanes anubus</i>	.69	.08	10	.80		1
<i>Xylophanes ceratomioides</i>	.79	.12	5	1.19		1
<i>Xylophanes chiron</i>	.69		1			
<i>Xylophanes libya</i>	.45	.08	6	.69		1
<i>Xylophanes maculator</i>	.44	.02	4			
<i>Xylophanes pluto</i>	.42	.06	10	.64	.19	7
<i>Xylophanes porcus</i>	.60	.07	10	.70		1
<i>Xylophanes tersa</i>	.38	.06	9	.61		2
<i>Xylophanes turbata</i>	.45	.10	10	.62	.13	9
<i>Xylophanes tyndarus</i>	.78		1			
* <i>Xylophanes</i> sp.						
Range	.14-3.28			.35-4.58		

Table 3

Saturniidae larval hosts in nature in Santa Rosa National Park (as of December 1983).

Arsenurinae

<i>Arsenura armida</i>	<i>Bombacopsis quinatum</i> (Bombacaceae)	large tree crown
<i>Caio championi</i>	<i>Bombacopsis quinatum</i> (Bombacaceae)	large tree crown
<i>Copiopteryx semiramis</i>	<i>Manilkara chicle</i> (Sapotaceae)	large tree crown
<i>Dysdaemonia boreas</i>	<i>Ceiba pentandra</i> (Bombacaceae) ¹	large tree crown
<i>Tiataea tamerlan</i>	<i>Bombacopsis quinatum</i> (Bombacaceae)	large tree crown

Ceratocampinae

<i>Adeloneivaia isara</i>	<i>Lysiloma divaricata</i> (Leguminosae)	large tree crown
	<i>Lysiloma auritum</i> (Leguminosae)	large tree crown
<i>Citheronia bellavista</i>	<i>Phoradendron quadrangulare</i> (Loranthaceae) ²	parasite in crown of large tree
<i>Citheronia lobesis</i>	<i>Cochlospermum vitifolium</i> (Cochlospermaceae)	large saplings
	<i>Bursera simaruba</i> (Burseraceae)	large tree crown
	<i>Spondias mombin</i> (Anacardiaceae)	large saplings
	<i>Psidium guajava</i> (Myrtaceae) ³	shrubby treelet
	<i>Calcyophyllum candidissimum</i> (Rubiaceae)	large tree crown
	<i>Phoradendron quadrangulare</i> (Loranthaceae)	parasite in crown of large tree
<i>Eacles imperialis</i>	<i>Cochlospermum vitifolium</i> (Cochlospermaceae)	large saplings and large tree crown
	<i>Bursera tomentosa</i> (Burseraceae)	large tree crown
	<i>Astronium graveolens</i> (Anacardiaceae)	large tree crown
	<i>Cedrela odorata</i> (Meliaceae)	large tree crown
<i>Othorene purpurascens</i>	<i>Manilkara chicle</i> (Sapotaceae)	large tree crown
<i>Othorene verana</i>	<i>Quercus oleoides</i> (Fagaceae)	large tree crown
<i>Ptiloscota dargei</i>	<i>Acacia tenuifolia</i> (Leguminosae)	saplings and large vine crown
<i>Schausiella santarosensis</i>	<i>Hymenaea courbaril</i> (Leguminosae)	large tree crown

<i>Syssphinx colla</i>	<i>Pithecellobium saman</i> (Leguminosae)	large tree crown
<i>Syssphinx mexicana</i>	<i>Acacia collinsii</i> (Leguminosae)	sapling to adult treelet crown
	<i>Acacia cornigera</i> (Leguminosae)	sapling to adult treelet crown
<i>Syssphinx molina</i>	<i>Pithecellobium saman</i> (Leguminosae)	large tree crown
	<i>Cassia grandis</i> (Leguminosae) ³	large tree crown
	<i>Albizzia adinocephala</i> (Leguminosae)	large tree crown
<i>Syssphinx quadrilineata</i>	<i>Acacia collinsii</i> (Leguminosae) ²	laboratory
Hemileucinae		
<i>Automeris io</i>	<i>Crescentia alata</i> (Bignoniaceae) ³	large tree crown
	<i>Mimosa pigra</i> (Leguminosae)	shrub
	<i>Cassia biflora</i> (Leguminosae)	shrub
	<i>Rhynchosia reticulata</i> (Leguminosae)	herbaceous vine
	<i>Gliricidia sepium</i> (Leguminosae)	sapling
<i>Automeris rubrescens</i>	<i>Inga vera</i> (Leguminosae)	sapling
	<i>Rourea glabra</i> (Connaraceae)	scandent shrub
	<i>Guazuma ulmifolia</i> (Sterculiaceae)	large tree crown
	<i>Cassia biflora</i> (Leguminosae)	shrub
	<i>Quercus oleoides</i> (Fagaceae)	sapling
	<i>Cordia alliodora</i> (Boraginaceae)	sapling
	<i>Lonchocarpus minimiflorus</i> (Leguminosae)	sapling
	<i>Calycophyllum candidissimum</i> (Rubiaceae)	large tree crown
	DHJ 12175 (Bignoniaceae)	sapling vine
	<i>Zuelania guidonia</i> (Flacourtiaceae)	large tree crown
	<i>Crescentia alata</i> (Bignoniaceae) ³	large tree crown
	<i>Cassia grandis</i> (Leguminosae)	large tree crown
<i>Automeris zugana</i>	<i>Annona purpurea</i> (Annonaceae)	large tree crown
	<i>Lonchocarpus costaricensis</i> (Leguminosae)	large tree crown
	<i>Quercus oleoides</i> (Fagaceae)	large tree crown
	<i>Cydista heterophylla</i> (Bignoniaceae)	large woody vine
	<i>Calycophyllum candidissimum</i> (Rubiaceae)	sapling to large tree crown

	<i>Hymenaea courbaril</i> (Leguminosae)	sapling
	<i>Solanum hazenii</i> (Solanaceae)	large herb
	<i>Lantana camara</i> (Verbenaceae) ³	large herb/shrub
	<i>Lonchocarpus eriocarinalis</i> (Leguminosae)	large tree crown
	<i>Centrosema pubescens</i> (Leguminosae)	herb vine
	<i>Cassia hayesiana</i> (Leguminosae)	shrub/treelet
	<i>Inga vera</i> (Leguminosae)	sapling
	<i>Serjania atrolineata</i> (Sapindaceae)	large vine
<i>Dirphia avia</i>	<i>Hymenaea courbaril</i> (Leguminosae)	large tree crown
	<i>Cedrela odorata</i> (Meliaceae)	large tree crown
<i>Hylesia dalina</i>	<i>Casearia arguta</i> (Flacourtiaceae)	treelet
	<i>Malvaviscus arboreus</i> (Malvaceae)	shrub
<i>Hylesia lineata</i>	<i>Tabebuia rosea</i> (Bignoniaceae)	sapling
	<i>Bombacopsis quinatum</i> (Bombacaceae)	large tree crown
	<i>Cordia alliodora</i> (Boraginaceae)	treelet
	<i>Hirtella racemosa</i> (Chrysobalanaceae)	treelet
	<i>Muntingia calabura</i> (Elaeocarpaceae)	treelet
	<i>Casearia arguta</i> (Flacourtiaceae)	treelet
	<i>Casearia sylvestris</i> (Flacourtiaceae)	treelet
	<i>Casearia corymbosa</i> (Flacourtiaceae)	treelet
	<i>Zuelania guidonia</i> (Flacourtiaceae)	large tree crown
	<i>Acacia tenuifolia</i> (Leguminosae)	large vine crown
	<i>Cassia biflora</i> (Leguminosae)	shrub
	<i>Diphysa robinioides</i> (Leguminosae)	sapling
	<i>Enterolobium cyclocarpum</i> (Leguminosae)	large tree crown
	<i>Hymenaea courbaril</i> (Leguminosae)	sapling
	<i>Inga vera</i> (Leguminosae)	treelet
	<i>Lonchocarpus minimiflorus</i> (Legumin.)	treelet
	<i>Lonchocarpus costaricensis</i> (Legumin.)	sapling
	<i>Lysiloma auritum</i> (Leguminosae)	large tree crown

<i>Machaerium kegelii</i> (Leguminosae)	sapling large vine
<i>Mimosa pigra</i> (Leguminosae)	shrub
<i>Myrospermum frutescens</i> (Leguminosae)	treelet
<i>Pithecellobium lanceolatum</i> (Legumin.)	treelet
<i>Hyptis pectinata</i> (Labiatae)	large herb
<i>Malvaviscus arboreus</i> (Malvaceae)	shrub
<i>Banisteriopsis muricata</i> (Malpighiaceae)	low vine
<i>Byrsonima crassifolia</i> (Malpighiaceae)	treelet
<i>Stigmaphyllon ellipticum</i> (Malpighiaceae)	low vine
<i>Psidium guineense</i> (Myrtaceae)	shrub
<i>Ouratea lucens</i> (Ochnaceae)	shrub
<i>Gouania polygama</i> (Rhamnaceae)	low vine
<i>Calycophyllum candidissimum</i> (Rubiaceae)	sapling
<i>Chomelia spinosa</i> (Rubiaceae)	treelet
<i>Guetarda macrosperma</i> (Rubiaceae)	treelet
<i>Xanthoxylum setulosum</i> (Rutaceae)	sapling
<i>Allophylus occidentalis</i> (Sapindaceae)	treelet
<i>Cupania guatemalensis</i> (Sapindaceae)	treelet
<i>Paullinia cururu</i> (Sapindaceae)	low vine
<i>Serjania schiedeana</i> (Sapindaceae)	low vine
<i>Urvillea ulmacea</i> (Sapindaceae)	low vine
<i>Byttneria aculeata</i> (Sterculiaceae)	shrub
<i>Byttneria catalpaefolia</i> (Sterculiaceae)	low vine
<i>Guazuma ulmifolia</i> (Sterculiaceae)	medium tree
<i>Luehea speciosa</i> (Tiliaceae)	sapling
<i>Lantana camara</i> (Verbenaceae) ³	shrub
<i>Erythroxylum havanense</i> (Erythroxylaceae)	shrub
<i>Calliandra emarginata</i> (Leguminosae)	shrub
<i>Eugenia salamensis</i> (Myrtaceae)	medium tree crown
<i>Cassia biflora</i> (Leguminosae)	shrub
<i>Periphoba arcae</i>	

	<i>Guazuma ulmifolia</i> (Sterculiaceae)	large tree crown
	<i>Lysiloma auritum</i> (Leguminosae)	large tree crown
	<i>Spondias mombin</i> (Anacardiaceae)	large tree crown
	<i>Rourea glabra</i> (Connaraceae)	scandent shrub
	<i>Annona purpurea</i> (Annonaceae)	treelet crown
	<i>Calycophyllum candidissimum</i> (Rubiaceae)	large tree crown
	<i>Bombacopsis quinatum</i> (Bombacaceae)	large tree crown
	<i>Cassia alata</i> (Leguminosae) ³	large tree crown
	<i>Inga vera</i> (Leguminosae)	medium tree crown
	<i>Ardisia revoluta</i> (Myrsinaceae)	treelet
	<i>Astronium graveolens</i> (Anacardiaceae)	sapling
	<i>Hymenaea courbaril</i> (Leguminosae)	sapling
	<i>Quercus oleoides</i> (Fabaceae)	large tree crown
	<i>Miconia argentea</i> (Melastomataceae)	sapling
Saturniinae		
	<i>Copaxa moinieri</i>	saplings and lower branches of treelet
	<i>Rothschildia erycina</i>	large tree crown
	<i>Coutarea hexandra</i> (Rubiaceae)	treelet crown
	<i>Rothschildia lebeau</i>	large tree crown
	<i>Exostema mexicanum</i> (Rubiaceae)	large tree crown
	<i>Spondias mombin</i> (Anacardiaceae)	treelet
	<i>Spondias purpurea</i> (Anacardiaceae)	treelet
	<i>Casearia corymbosa</i> (Flacourtiaceae)	treelet
	<i>Zuelania guidonia</i> (Flacourtiaceae)	large tree crown
	<i>Xanthoxylum setulosum</i> (Rutaceae)	large tree crown

¹ Not found in nature but accepts readily and dies on other Santa Rosa Bombacaceae. ² Not found in nature but accepts readily and has the appropriate colour and behaviour to use this host. ³ Plant introduced to Santa Rosa within past several hundred years.

determined by both immediate environmental factors and internal calendars, and larval size is highly variable within a species at the time of pupation. Sex ratios of first instar larvae and of wild-caught caterpillars are one to one.

For the purpose of this essay the focal characteristics of saturniids are that they do not feed as adults, are short-lived as adults, and have caterpillars with diverse and sometimes lengthy host lists. The adult males are primarily specialists at locating females, and the females are specialized for oviposition (and staying alive long enough to do so). They both experience selection for escape from predators, but the selective pressures are probably different because of differences in weight, size, habitat needs, rate of potential fitness loss with age, *etc.*

Sphingid caricature

Body weights of adult sphingid moths of Santa Rosa (Figs. 3–4) are distributed over about the same range as are those of the saturniids (Table 2). The 63 species that breed in the Park (and the 16 transient species) also have about the same aggregate geographic range (e.g., Schreiber 1978) as do the saturniids, except that the sphingids also occur on many Caribbean and Pacific Islands (e.g., Cary 1957, Curio 1965) while saturniids are generally absent from the islands in the New World. While the three species of *Aellopos* are diurnally active, the remaining Santa Rosa sphingids are nocturnal, as are the saturniids. All the nocturnal and crepuscular species are highly cryptic when at rest in the daytime (bark and damaged leaf colours and patterns, just as with saturniids), but all display red, yellow or white presumed flash colours on the hind wings and body when fleeing. Both sexes regularly drink with a long proboscis from many kinds of flowers while hovering in front of them (e.g., Haber and Frankie 1984, Bullock and Pescador 1983), presumably to obtain water as well as nutrients. Females generally weigh one to two times as much as do males at the time of eclosion, but owing to variation in the amount of oviposition and nectar uptake, middle-aged adult conspecific sphingids of both sexes are often of similar body weight (Table 2). Newly eclosed adults climb upward a few decimetres to hang and expand their wings, but generally do not fly on the night of eclosion. Mating probably occurs some days later, and is multiple for females (W. Haber, personal communication) and probably males. Oviposition ranges from rapid production of eggs, such that all the eggs may be laid within as short a time as a week (e.g., *Aellopos titan*, Janzen 1984b) to an oviposition period of weeks to months with only a few eggs maturing nightly (W. Haber, personal communication). Fecundity is unknown but probably in the hundreds if the female can feed freely.

The eggs hatch in four to eight days and are never the stage that passes the Santa Rosa five-month dry season. Larval host plants (Table 4) range from annual herbs to the crowns of large trees and vines; many are vines, small plants and juveniles of large plants. Caterpillars of many species of

Table 4

Sphingidae larval hosts in Santa Rosa National Park (as of December 1983).

<i>Aellopos clavipes</i>	<i>Randia karstenii</i> (Rubiaceae)	sapling to treelet
<i>Aellopos fadus</i>	<i>Genipa americana</i> (Rubiaceae)	sapling to large tree
	<i>Alibertia edulis</i> (Rubiaceae)	shrub
<i>Aellopos titan</i>	<i>Randia karstenii</i> (Rubiaceae)	sapling to treelet
	<i>Randia subcordata</i> (Rubiaceae)	sapling to treelet
<i>Agrius cingulatus</i>	<i>Merremia umbellata</i> (Convolvulaceae)	herb vine
	DHJ 12071 (Convolvulaceae)	herb vine
<i>Aleuron carinata</i>	<i>Doliocarpus dentatus</i> (Dilleniaceae)	low perennial vine
<i>Aleuron iphis</i>	<i>Tetracera volubilis</i> (Dilleniaceae)	low perennial vine
<i>Amplipterus gannascus</i>	<i>Ocotea veraguensis</i> (Lauraceae)	sapling to treelet
<i>Amplipterus ypsilon</i>	<i>Ocotea veraguensis</i> (Lauraceae)	sapling to treelet
<i>Callionima falcifera</i>	<i>Stemmadenia obovata</i> (Apocynaceae)	sapling to treelet
<i>Cautethia spuria</i>	<i>Exostema mexicanum</i> (Rubiaceae)	sapling to large tree
	<i>Coutarea hexandra</i> (Rubiaceae)	treelet
<i>Cautethia yucatanana</i>	<i>Exostema mexicanum</i> (Rubiaceae)	treelet
<i>Cocytius duponchel</i>	<i>Annona purpurea</i> (Annonaceae)	sapling to treelet
	<i>Annona reticulata</i> (Annonaceae)	sapling to treelet
<i>Enyo ocypete</i>	<i>Tetracera volubilis</i> (Dilleniaceae)	low perennial vine
	<i>Ciccus rhombifolia</i> (Vitaceae)	herb vine
<i>Erinnyis ello</i>	<i>Sebastiania confusa</i> (Euphorbiaceae)	sapling to treelet
	<i>Sapium thelocarpum</i> (Euphorbiaceae)	sapling
	<i>Manilkara chicle</i> (Sapotaceae)	large tree
<i>Erinnyis lassauxii</i>	<i>Sarcostemma glauca</i> (Asclepiadaceae)	low vine
<i>Erinnyis oenotrus</i>	<i>Forsteronia spicata</i> (Apocynaceae)	low perennial vine
<i>Eumorpha anchemola</i>	<i>Cissus rhombifolia</i> (Vitaceae)	low perennial vine
	<i>Cissus sicyoides</i> (Vitaceae)	low perennial vine

<i>Eumorpha satellitia</i>	<i>Cissus rhombifolia</i> (Vitaceae)	low perennial vine
	<i>Cissus sicyoides</i> (Vitaceae)	low perennial vine
<i>Eupyrrhoglossum sagra</i>	<i>Chomelia spinosa</i> (Rubiaceae)	sapling to treelet
	<i>Guettarda macrosperma</i> (Rubiaceae)	sapling to treelet
<i>Isognathus rimosus</i>	<i>Plumeria rubra</i> (Apocynaceae)	large tree
<i>Manduca barnesi</i>	<i>Godmania aesculifolia</i> (Bignoniaceae)	sapling
<i>Manduca corallina</i>	<i>Cordia alliodora</i> (Boraginaceae)	sapling to large tree
<i>Manduca dilucida</i>	<i>Sapranthus palanga</i> (Annonaceae)	sapling to treelet
	<i>Annona reticulata</i> (Annonaceae)	sapling to treelet
<i>Manduca florestan</i>	<i>Pithecoctinium crucigerum</i> (Bignoniaceae)	low perennial vine
	<i>Cydista heterophylla</i> (Bignoniaceae)	low perennial vine
	<i>Tabebuia ochracea</i> (Bignoniaceae)	sapling
	<i>Callichlamys latifolia</i> (Bagnoniaceae)	low perennial vine
	<i>Arrabidaea chica</i> (Bignoniaceae)	low perennial vine
	<i>Cornutia grandifolia</i> (Verbenaceae)	shrub
	<i>Ceratophytum tetragonolobum</i> (Bignoniaceae)	low perennial vine
	<i>Pleonotoma variabilis</i> (Bignoniaceae)	low perennial vine
	<i>Stachytarpheta frantzii</i> (Verbenaceae)	shrub
<i>Manduca lefeburei</i>	<i>Casearia sylvestris</i> (Flacourticeae)	sapling to treelet
	<i>Casearia corymbosa</i> (Flacourticeae)	sapling to treelet
<i>Manduca muscosa</i>	<i>Verbesina gigantea</i> (Compositae)	giant herb
	<i>Lantana camara</i> (Verbenaceae) ¹	shrub
	<i>Lasianthaea fruticosa</i> (Compositae)	shrub
	<i>Baltimora recta</i> (Compositae)	herb
	<i>Melanthera aspera</i> (Compositae)	herb
	<i>Wedelia calycina</i> (Compositae)	herb
<i>Manduca occulta</i>	<i>Solanum ochraceo-ferrugineum</i> (Solanaceae)	herb
	<i>Solanum hazenii</i> (Solanaceae)	herb
	<i>Solanum accrescens</i> (Solanaceae)	herb
	<i>Cestrum</i> DHJ 12029 (Solanaceae)	shrub

<i>Manduca rustica</i>	<i>Lantana camara</i> (Verbenaceae) ¹	shrub					
	<i>Stachytarpheta frantzii</i> (Verbenaceae)	shrub					
	<i>Cordia panamensis</i> (Boraginaceae)	sapling					
	<i>Pithecoctenium crucigerum</i> (Bignoniaceae)	low perennial vine					
	<i>Amphilophium paniculatum</i> (Bignoniaceae)	low perennial vine					
	<i>Merremia umbellata</i> (Convolvulaceae)	herb vine					
	DHJ 12071 (Convolvulaceae)	herb vine.					
	<i>Hyptis verticillata</i> (Labiatae)	herb					
	<i>Manduca sexta</i>	<i>Capsicum annum</i> (Solanaceae)	herb				
		<i>Lycopersicon esculentum</i> (Solanaceae) ¹	herb				
<i>Piper marginatum</i> (Piperaceae)		shrub					
<i>Neococytius cluentius</i>		<i>Calycophyllum candidissimum</i> (Rubiaceae)	sapling to large tree				
		<i>Nyceryx coffeae</i>	<i>Doliocarpus dentatus</i> (Dilleniaceae)	low perennial vine			
			<i>Pachygonia drucei</i>	<i>Ficus insipida</i> (Moraceae)	sapling to large tree		
				<i>Ficus cotinifolia</i> (Moraceae)	sapling to large tree		
				<i>Ficus obtusifolia</i> (Moraceae)	sapling to large tree		
				<i>Ficus ovalis</i> (Moraceae)	sapling to large tree		
				<i>Brosimum alicastrum</i> (Moraceae)	sapling		
	<i>Chlorophora tinctoria</i> (Moraceae)			sapling to large tree			
	<i>Pachylyia ficus</i>			<i>Castilla elastica</i> (Moraceae)	sapling		
				<i>Ficus ovalis</i> (Moraceae)	large tree		
<i>Pachylyia syces</i>				<i>Forsteronia spicata</i> (Apocynaceae)	low perennial vine		
		<i>Pachyliooides resumens</i>		<i>Calcyphyllum candidissimum</i> (Rubiaceae)	sapling to large tree		
			<i>Guettarda macrosperma</i> (Rubiaceae)	sapling to treelet			
			<i>Protambulyx strigilis</i>	<i>Astronium graveolens</i> (Anacardiaceae)	sapling to large tree		
				<i>Spondias mombin</i> (Anacardiaceae)	sapling to large tree		
				<i>Pseudosphinx tetrio</i>	<i>Plumeria rubra</i> (Apocynaceae)	large tree	
					<i>Sphinx merops</i>	<i>Lantana camara</i> (Verbenaceae) ¹	shrub
						<i>Hyptis pectinata</i> (Labiatae)	herb

<i>Unzela pronoe</i>	<i>Tetracera volubilis</i> (Dilleniaceae)	low perennial vine
<i>Xylophanes anubus</i>	<i>Psychotria nervosa</i> (Rubiaceae)	shrub
	<i>Psychotria horizontalis</i> (Rubiaceae)	shrub/herb
<i>Xylophanes ceratomioides</i>	<i>Hamelia patens</i> (Rubiaceae)	shrub
<i>Xylophanes chiron</i>	<i>Psychotria pubescens</i> (Rubiaceae)	shrub
	<i>Psychotria horizontalis</i> (Rubiaceae)	shrub
	<i>Faramea occidentalis</i> (Rubiaceae)	sapling
<i>Xylophanes juanita</i>	<i>Psychotria pubescens</i> (Rubiaceae)	shrub
	<i>Psychotria horizontalis</i> (Rubiaceae)	shrub/herb
	<i>Psychotria nervosa</i> (Rubiaceae)	shrub
<i>Xylophanes maculator</i>	<i>Psychotria horizontalis</i> (Rubiaceae)	shrub/herb
<i>Xylophanes pluto</i>	<i>Hamelia patens</i> (Rubiaceae)	shrub
<i>Xylophanes porcus</i>	<i>Hamelia patens</i> (Rubiaceae)	shrub
<i>Xylophanes turbata</i>	<i>Hamelia patens</i> (Rubiaceae)	shrub to treelet
	<i>Psychotria mecrodon</i> (Rubiaceae)	shrub/herb
<i>Xylophanes tyndarus</i>	<i>Faramea occidentalis</i> (Rubiaceae)	treelet

¹ Host plant introduced to Santa Rosa National Park.

sphingids eat both young and mature leaves. If a Santa Rosa sphingid has two or more larval host species, they are almost always closely related at the level of the family or genus (Table 4). None has legumes as host plants, and in general they eat a different subset of the Santa Rosa flora than do the saturniids. The Santa Rosa sphingids not only have enormous latitudinal ranges, but also most occur in many other Costa Rican habitats (as is the case with the saturniids); over these ranges they tend to have the same or closely related larval host plants (e.g., Moss 1912, 1920, Hodges 1971, W. Haber, personal communication). Larvae use two to five weeks for larval development and are subject to the same kinds of mortality as are saturniids, but in different proportions. Sphingid larvae occasionally defoliate individuals or populations of their larval hosts (e.g., Janzen 1981, 1984b). All but *Pseudosphinx tetrio*, which is either aposematic or a coral snake mimic (Janzen 1983), are highly cryptic at rest; a few (*Xylophanes* spp., *Hemeroplanes triptolemus*, *Eumorpha labruscae*, *Erinnyis ello*, *Agrius cingulatus*) become mimetic of vertebrate eyes when attacked. Almost all cryptic species have larval polymorphisms within and among instars (e.g. Schneider 1973). The last instar makes its pupation chamber underground or in the litter. The pupal stage lasts two to many weeks, is variable in length within a species and season, and is the stage that passes the dry season except for those sphingids that have continuous generations throughout the year (e.g., *Pachylia ficus*, *Protambulyx strigilis*, *Cautethia spuria*) or leave the Park for part of the year (e.g., *Aellopos titan*, Janzen 1984b). Larval duration is variable and determined by both environmental factors and internal calendars. Primary sex ratios are as in saturniids, one to one.

The key sphingid trait, in contrast with saturniids, is that adult sphingids feed heavily over a long period and possess the mental and flight machinery to do it. Sphingids of opposite sexes and of different species therefore have a major activity in common – finding flowers, hovering in front of those flowers, using the resources so gained, and remembering where those flowering plants are the next night.

Santa Rosa as a saturniid and sphingid habitat

The Park (10 degrees north Latitude) is a fine-scale mosaic of deciduous to evergreen forest ranging from newly abandoned grassy pastures and old fields to virtually pristine forests. Plant species richness ranges from nearly monospecific tree stands (mangroves, evergreen *Hymenaea* or *Quercus* forest) to 20–30 species of woody plants per ha (dry rocky cactus-rich ridges) to 100-plus species of woody plants per ha (late succession on good soil); there are about 650 breeding dicot plant species in the Park (Janzen and Liesner 1980). Spanning 0–350 m elevation, it is primarily a habitat and climate representative of the pre-Columbian Central American Pacific coastal plain with intrusions from the more moist volcanic foothills immediately adjacent to the Park (Boza and Mendoza 1981, Hartshorn 1983). The five-month long rain-free dry season ends with varying suddenness in May, a variably light and short dry season occurs in late

July—early August, and the rains terminate between late November and early January. Between 900 and 2200 mm of rain fall during the rainy season, and the dry season is generally so windy and sunny that it can kill an exposed first instar saturniid caterpillar by desiccation in a single day.

Santa Rosa's deciduous forest climate (and the 4000-plus km² of similar Costa Rican climate in which it is embedded) contrasts strongly with the wetter evergreen rainforest habitats covering most of the remainder of the country (Hartshorn 1983, Coen 1983). The deciduous forest vegetation of Costa Rica likewise differs from the rainforest in that the former has been almost entirely replaced by the biological deserts of croplands and pastures, while there is still enough of the latter to make a conservation effort worthwhile.

The saturniid (Janzen 1982) and sphingid (Haber 1983) faunas of Santa Rosa are very similar in species richness, composition and relative abundance to those of other Central American and lowland tropical Mexican deciduous forest habitats (e.g. Beutelspacher 1978, 1981, Hoffman 1942). They differ from those of the lowland rainforest parts of Costa Rica by being about 20 per cent less species rich, proportionately and absolutely richer in what are traditionally thought of as extra-tropical and arid-land species and genera of moths, and much more seasonal in periodicity of abundance. For example, there are 12 species of Ceratocampinae breeding at Santa Rosa but only 10 breeding Hemileucinae; at Costa Rican lowland rainforest sites, there are usually eight to 10 Ceratocampinae and 15–20 Hemileucinae. Likewise, at rainforest sites most species are present as adults year round, while all Santa Rosa saturniid populations are dormant from January to the end of April.

Santa Rosa has a substantial fauna of carnivores that feed on saturniid and sphingid caterpillars and adults. In addition to the generally insectivorous birds, bats, insectivores and small rodents found in any mesic forest, there are squirrel cuckoos (*Piaya cayana*) that specialize on finding and eating large urticating caterpillars (e.g., *Hylesia lineata*, *Dirphia avia*, *Automeris zugana*), armadillos (*Dasybus novemcinctus*) and coatis (*Nasua narica*) that plough up the litter in search of caterpillars and pupae, white-faced capuchin monkeys (*Cebus capucinus*) that glean the forest from about four metres to the tops of the tallest crowns, and arboreal mice (e.g., *Reithrodontomys gracilis*) that glean larvae, pupae and adults at night. However, in contrast with extra-tropical moth-rich forests, there is no massive invasion of migrant insectivorous small birds during the rainy (caterpillar breeding) season. In addition to the expected fauna of spiders, scorpions, predacious bugs, ants, wasps, tettigoniid grasshoppers and crickets, there is an abundant but species-poor fauna of parasitic Hymenoptera and tachnid flies. Viral, bacterial and fungal diseases are conspicuous sources of caterpillar death (e.g., Janzen 1984a).

Some of the key quantitative features of Santa Rosa as a saturniid and sphingid habitat are, then, a five- to seven-month rainy season that is long enough for two to three generations of most species, a dry season sufficiently severe to cause most species to be dormant (saturniids and sphingids) or migrate (some sphingids) even if they feed on evergreen

hosts, hundreds of broad-leaved plant species within normal flight range of an individual of any moth species, a rich carnivore array, and highly variable timing of the onset and intensity of the rainy season. The abrupt and dramatic change in weather with the onset of the rains in late April or early May serves as a major synchronization cue for moth populations, a cue somewhat analogous to an extra-tropical spring. Each moth species is accompanied by an array of confamilials as great as that to be found in half of North America north of Mexico.

Differential attraction to lights

When saturniids and sphingids are collected throughout the year at a bright light (a 15 watt fluorescent and a 15-watt ultra violet-rich black light placed one metre apart on a white background) at Santa Rosa in or over a forested habitat, each of the families has a different pattern of appearance at the light. 90 per cent of the female saturniids arrive during the first four hours of the night and the females of no saturniid species regularly arrive after midnight. Except for the saturniid species whose females call in the first few hours after dark (*Dirphia avia*, *Adeloneivaia isara*, probably *Automeris zurobara*), the males arrive almost entirely during the second half of the night. On the same nights, provided a sphingid migration is not occurring, half or more of the species of sphingids arrives before midnight and females continue to arrive throughout the night. If a migration of sphingids is occurring (as opposed to a local population high), sex ratios may be equal or even strongly biased toward females. After coming to rest at the light, neither saturniids nor sphingids are likely to leave, but sphingids are more likely to leave than are saturniids. Throughout the rainy season the saturniids as species and in aggregate display stronger peaks and troughs in density and have less lunar phobia (as measured by arrival at lights). Saturniid fluctuations in numbers at lights correlate better with the density of adults in the habitat than is the case with sphingids. If saturniids and sphingids are marked at a light and released 50–100 m distant at dawn, the saturniids are more likely to reappear at the light during the next few nights than are the sphingids, but some of the sphingids will reappear as long as two to four weeks later.

Such differences as these, potentially mere artifacts since they are components of the larger artifact of arriving at a light, suggest major and revealing differences in the biology of saturniids and sphingids. To make this suggestion, I discuss a hypothesis on why moths arrive at lights and differences in the details of saturniid and sphingid natural history that could generate different arrival patterns.

Why do moths arrive at lights? This question is two questions. First, why does an adult moth released within one to five metres of a light often fly directly to it and come to rest nearby (Henton 1974, Weiss *et al.* 1941, Hsiao 1972)? All the Santa Rosa saturniids and sphingids that come to light display this behaviour, though certain individuals of certain species may also ignore a light (e.g., *Pachyliodes resumens* may fly in a controlled

manner up to a light and then fly away from it; a saturniid following a pheromone plume may fly right past a light, and a male saturniid going at full speed may careen so far past a light that it is carried into the dark before it can turn around and return). Despite some attempts at constructing a working hypothesis for this question (Hsiao 1972), there is neither a traditional nor avant-garde reasonable explanation of this behaviour. I have no convincing hypothesis to offer. This behaviour does not appear to be a disconnected fragment of moth biology, is generally not shown by diurnally active moths or butterflies (or caterpillars), and is exhibited by only a very small proportion of the non-lepidopteran insect species in the area of the light. Whatever the cause, this response is so useful for collectors and ecologists that moths should long ago have become one of the most studied of wild insects.

Second, why do (so many) moths arrive at the site of the light (at which point they are then directly attracted)? The thousands of moths of hundreds of species that often arrive at a light in one night at Santa Rosa certainly would not have accidentally flown that night through any one randomly placed two to five metre diameter hemispherical area of direct attraction. The current hypothesis, developed by R. R. Baker and foreshadowed by Robinson and Robinson (1950), is that a moth that needs to fly in a straight line can do this best by flying at a constant angle to a very distant landmark (e.g., moon, star, bright cloud) (Wehner 1984, Baker and Mather 1982; see also Baker and Sadovy 1978, Sothibandhu and Baker 1979). If, however, the landmark is a bright light hung in the forest (and therefore very near), the moth flying at a constant angle will trace a spiral path to it. It is striking that the lights used at Santa Rosa are indistinguishable to my eye from a bright star at a distance of 0.5–5 km.

A simpler edition of the above hypothesis is that the moth wishing to fly in a straight line selects the landmark which is directly ahead and homes on that. In this case a much smaller subset of the moths in the habitat would arrive at the light than if a more complex angular orientation were being used.

I accept that the light is a landmark to the moth as a working paradigm. The most biologically relevant question to this essay then becomes, why should a non-migratory adult saturniid or sphingid wish to fly in a straight line when not following an odour plume or wind current? I discuss this question only for saturniids and sphingids, but I assume that to some degree the discussion applies to other moths as well.

Why do Santa Rosa saturniids arrive at lights? This question is really a query about what determines the frequency with which saturniids fly in a straight line while using a landmark such as the light and also, just happen to fly through the hemisphere of direct attraction while doing other things. In other words, how do male saturniids search for females and how do females search for oviposition sites?

In the most direct sense male saturniids presumably find virgin female saturniids by flying upwind along a pheromone plume, just as do other moths (e.g., Kennedy *et al.* 1980, 1982, Collins and West 1961, Cardé and

Hargaman 1979, Tobin and Bell 1982, Baker and Kuenen 1982). But what is unknown is how insects in general, and saturniids specifically, search for pheromone plumes. For a moth with a short and fixed adult life, the worst method would be to sit and wait for the odour plume to arrive, and probably the next worst is to fly about at random. I therefore assume that male saturniids have species-specific search patterns for pheromone plumes. The searching male is faced with the following conditions. The plume lies downwind, turbulence is an inevitable consequence of wind flow through and over vegetation, competition is severe among males since there are many fewer virgin females than males on any given night (each night of the population's eclosion period adds more males but the nightly cohort of virginal females is removed by mating), and the pheromone plume is diluted with distance. The optimal search machine should fly rapidly at right angles to the general direction of the wind until a pheromone plume is encountered, and they fly upwind to the source with maximum haste. If no plume is encountered during a transit across the appropriate habitat, the moth should then drop downwind and repeat the process back across the same habitat. The distance downwind will depend on such things as the maximum distance at which a female can be perceived (considering the usual amount of turbulence and the consistency of the wind direction), the relative importance of finding the plume versus being able very quickly to move up it (the closer to the source the intersection, the quicker he can get to her), the patchiness of female-containing habitats, etc. Santa Rosa male saturniids have sustained flight airspeeds of 20–60 km per hour (the former speed is based on free-flying *Rothschildia lebeau* males released in calm air at dawn, and the latter speed is based on a free-flying male *Eacles imperialis* fortuitously flying parallel to a moving car in early dawn light). Capture-recapture records of males in traps baited with virgin females show numerous movements of two to six kilometres. I envision a given male regularly coursing over an area of several square kilometres during the second half of each night of its life (unless it finds a mate). If a bright light is placed on the horizon of that male's habitat, the moth should arrive at that light while searching, largely because it is using the light as a reference for flying a straight line at right angles to the general direction of the wind. However, it may also occasionally arrive at a light because its path just happens to intersect the tiny hemisphere of direct light influence.

Saturniid males are famous for eventually arriving at traps baited with virgin females after being released many kilometres away (e.g., Brower *et al.* 1967, Jeffords *et al.* 1980, Waldbauer and Sternburg 1982b, Rau and Rau 1929). This leads to the potentially deceptive impression that the males are 'attracted' to the females over these distances (Rau and Rau 1929, Riddiford 1974). The search-pattern hypothesis developed in the previous paragraph suggests that male saturniids might well be attracted only over quite short distances but have an effective and/or wide-ranging search pattern that eventually leads them to pass near the trap female even if released far away.

The proposed search pattern, and the moth's use of the light as a landmark, is compatible with many of the heterogeneities in arrivals of saturniids at lights at Santa Rosa. For example, the arrival time of male saturniids is synchronous with the calling times of their respective females. *Dirphia avia* begin to call just after sunset and the males arrive at the lights almost entirely within three hours after sunset. Females of the close relative *Periphoba arcaei* call shortly after midnight and the males arrive about that time. *Rothschildia lebeau* and *R. erycina* call during the two to three hours before dawn, and their males arrive at lights then. However, just as Waldbauer and Sternburg (1979) have observed with *Hyalophora cecropia* males in Illinois, the majority of Santa Rosa male saturniids that mate after midnight are also on the wing during the first couple of hours after sunset. They are not searching for females at this time (there are none calling), I favour Waldbauer's and Sternburg's (1979) hypothesis that they are moving to avoid mating with sisters, and they almost never arrive at the light at this time. I hypothesize that the occasional male of these species that arrives before 2200 hours (about three per cent of all males to arrive) is one that just happened to fly through the hemisphere of direct attraction by the light during its dispersal flight.

A second prominent heterogeneity is that except for *Rothschildia erycina* tens (*Adeloneivaia isara*, *Caio championi*) to hundreds (*Automeris zugana*, *Othorene purpurascens*) of males arrive for each female that arrives. Why are so many more male than female saturniids encountered at lights (as has also been observed elsewhere, e.g., Worth 1979, van den Berg 1973, 1974c)? First, males fly much farther than do females, and therefore any kind of point trap will intercept more per night. Second, many males will arrive at a light because they are using it as a landmark. Third, I do not expect the female saturniids to use the light for flight orientation.

Since the female pupates and mates directly below her larva's host plant, I assume that she first searches for larval food plants largely by flying a very local search pattern (e.g., by flying up host plant odour plumes even if quite faint). When less heavily egg-laden, she may fly farther but still very locally. Since saturniid females usually oviposit in the crowns of large adult perennials (the non-hemileucines and some hemileucines) or a few times per female in multi-species assemblages of large and small plants (some hemileucines), there is likely to be one or more host plants within a few metres of where mating occurred and others are likely to be within a 50–100 m radius. In such a scenario female saturniids should arrive at a light only if they happen to fly through its zone of direct influence; they should also arrive only during the first four to five hours of the evening, which is the case (in the laboratory, all 27 species of Santa Rosa saturniids observed oviposit in the first three hours after sunset). Only zero to three females of a particular species should be captured per light per night (unless there is a population high, e.g., *Hylesia lineata*, Janzen 1981, 1984a) because the local density of females is very low. Their numbers at lights may be even further reduced if they are as strongly attracted to a nearby oviposition site as are males to a nearby virgin female; such a male

can sometimes fly within a metre of the light without being attracted. In effect, the light is a very local census device for female saturniids but it censuses males over a much larger area.

I have no reason to expect any of the above processes to change with age of the male, since he cannot learn where his resources are clumped locally; virgin females will appear at different microsites each night, and he should at best only encounter one per night with even the best of luck. He should be just as susceptible to being pulled into the light on his first as his last night of flight. However, as his body weight declines (e.g., Waldbauer *et al.* 1984), he may be able to fly faster (further per night) with the result of more old males appearing at the light than young ones; such a numerical result will, however, be confounded by the fact that a cohort is always largest the night of its eclosion. The process might change with age of the female if she flies further as her egg load becomes lighter. However, so few females arrive at Santa Rosa lights (average about one per night per light, summed over all 30 species, during the rainy season) that it will require many more years of data for a picture to emerge.

Nevertheless, I do expect different species of saturniids to conform differently to this process of arrival at the lights. There should be species-specific variation in distance of direct attention, use of visual landmarks (is this why *Rothschildia erycina* males almost never come to the light at Santa Rosa?), distance flown in searching, fidelity to the microhabitat in which the light happens to be placed, etc.

What factors may be responsible for the frequent strong intra-specific night-to-night variation in numbers of male saturniids to arrive at Santa Rosa lights? Migration effects can be disregarded as there is no hint of migratory movements like those of the sphingids. First, if a virgin female happens to be calling within a few tens of metres of the light, an exceptional number of males may appear at the light. For example, during the 1981 population explosion of *Copaxa moinieri*, a forest understory light attracted one to five males each night of a three week period, except for three non-consecutive nights of 21, 37 and 34 males each (Janzen 1984d). During two of those nights I had hung a virgin female *C. moinieri* in deep shadow eight metres from the light. While many of the males arrive at a virgin female calling near a light ignore that light, they later end up perched at it.

Second, there should be a decline in numbers of males at lights on the nights of heavy female eclosion, since these males will spend more time flying upwind on pheromone plumes and will be trapped by the virgin females they encounter. On nights after most of the virgin females have eclosed and mated, there should be an excess of males searching the habitat.

Third, short-term inimical bad weather will generate heterogeneity, a heterogeneity that a male saturniid can not afford to conquer by inactivity, since it has so few days to live. On the one hand the more natural landmarks are obscured (by clouds, rain, fog, etc.), the more important is the light as a landmark (hence the huge catches at lights on a heavily foggy night). On the other hand a starry sky or bright moon offers many

landmarks to compete with the artificial light. Saturniids do display the phenomenon of lunar phobia, but not nearly as strongly as do sphingids (see below). If the air is very still, or the wind changes direction so frequently that pheromone plumes are chaotic in direction, there may be no advantage to straight flight and the male moths may use a different search pattern. Finally, the heterogeneity in time and space of eclosion cues will generate inter-night heterogeneity of the number of moths available to arrive at the lights; the shorter the life of the male moths, the more consequential will be this effect.

An arrival hypothesis helps to explain strong inter-site heterogeneity in numbers of moths arriving at several lights, even when they are only a few tens of metres apart. A light that is positioned near the horizon of the visual fields for a maximum number of searching males is likely to attract more males than will a light placed in other parts of the moths' visual fields. A light within the habitat in which males search for females will capture more males than will one that is visible to the moths in that habitat yet outside of it. A light placed among the crowns of potential larval hosts will catch more females than will one placed at a site that is often flown across by males. For example, one of the Santa Rosa lights is on a cliff top at the level of the crowns of nearby large *Bombacopsis quinatum* trees; this light captures more female *Caio championi* than male *C. championi*, presumably because the females fly near it when moving among the crowns of their sole species of host tree. On the other hand, a light placed in or near a migratory flyway – such as in the pass in a mountain chain (e.g., the famed Rancho Grande moth collecting site in Venezuela, Fleming 1947) – should capture migratory species of moths in enormous numbers (see below), but will not collect exceptional numbers of saturniids.

Why do Santa Rosa sphingids arrive at lights? In general the Santa Rosa sphingids should arrive at lights for the same behavioural reasons as do saturniids. However, sphingids differ from saturniids in several aspects of their natural history that should cause their arrival patterns to be quantitatively different. The relevant differences are that sphingids feed extensively at spatially particulate resources that are relatively fixed in location, live for weeks to months as adults, lay few eggs per night, probably oviposit on many host individuals and repeatedly visit many of them, have less synchronous eclosion during the rainy season, migrate, and are 'smarter' than are saturniids.

When the rains begin at the end of the long dry season in Santa Rosa's dry forests, a large number of sphingid individuals and species appear at the lights; one light may nightly attract several hundred individuals including 10–20 species. Within a few weeks, the numbers for each species declines to zero or to the low but fluctuating numbers that arrive at the lights throughout the remainder of the rainy season. There are two causes for the decline in numbers, only one of which also affects saturniids. Some of the species have laid their eggs and died, and the species is represented in the habitat by caterpillars (the saturniid life-style, albeit somewhat attenuated). However, from observations of caterpillar density, pupal

dormancy, and adults at flowers, it is clear that many of the species that cease to appear at the lights are still present as adults. For example, at one of the regular light stations there is a patch of *Stachytarpheta frantzii* (a verbenaceous heavily-visited shrubby nectar source for sphingids at Santa Rosa). It is 20–50 m behind the light and from it the light is clearly visible. At a time when *Erinnyis*, *Xylophanes*, *Enyo*, *Eumorpha*, *Pachylioides* and *Perigonia* have fallen to zero or very low density at this light, adults of both sexes of these species can be collected at the pre-dawn darkness while they drink nectar in the *S. frantzii* patch. On the other hand, these species and others whose nectar hosts are unknown to me continue to appear as very low numbers of newly eclosed individuals throughout the rainy season.

I hypothesize that for many of the Santa Rosa species of sphingids, individuals search widely at all hours of the night for the first few nights after eclosion, using lights for orientation but quickly learning where to find resources. Once they have established flight paths (using contour, odours, wind, ambient light and memory as cues), specific light landmarks are no longer used. It is striking that females become much scarcer than males at the lights very shortly after a species first appears seasonally; it may be that the males do search for females somewhat as do saturniid males. However, I suspect that they also use other search methods such as hill-topping familiar with butterflies and flies, repeated visits to areas where females are active (as in bees), patrolling mating territories (as in dragonflies), etc. When using a variety of chemical, memory and non-light landmarks to arrive at resources, both sexes of sphingids should become essentially immune to the distant attractiveness of an artificial light. As suggested by the common event of seeing a sphingid simply fly by a bright light at night with hardly any deviation, such experienced moths may even be immune to the close attractiveness of an artificial light. The above hypothesis is consistent with the observations that sphingids at Santa Rosa lights are often in fresh condition while conspecifics taken at flowers can be very worn as well as fresh. However, even the most experienced local sphingid may periodically become susceptible to an artificial light if it periodically undertakes straight-line exploratory flights to replenish fading resources or if a dense fog obliterates essentially all of its usual orientation cues.

The above model should be least applicable to species of sphingids that have relatively short adult life spans (e.g., some *Manduca*) and those that do not rely so heavily on nectar (e.g., perhaps *Amplypterus* and *Protambulyx*). From a practical viewpoint, such a model suggests that the most effective way to capture all the species of attractable sphingids in a habitat is to move the light from night to night, while for male saturniids there may be some best place to leave the light night after night.

At Santa Rosa, a number of crepuscular, matinal, and even fully nocturnal sphingids rarely or never appear at a light (e.g., six species of *Enyo*, *Aleuron*, *Eupyrrhoglossum* and *Pachygonia*). While the adults of these species are generally viewed as rare, the caterpillars can be annually or seasonally abundant. For example, I have found caterpillars of *Pachygonia drucei* and *Aleuron carinata* on *Doliocarpus dentatus* vines

growing only 40 m from a fixed light site at Santa Rosa; the females of these two species had to have been staring straight at the light as they oviposited yet the adults of these two species have never been found at any Santa Rosa light during about six light-years of maintaining the light. Over 2000 males and only one female of *Cautethia yucatanana* have been recorded at Santa Rosa lights in the same period. Such 'invisible' species are usually small and somewhat crepuscular or matinal; this may give them the ability to ignore the light and mean that they use dimly visible habitat contour as a primary means of orientation. Nevertheless, other small crepuscular sphingids, such as *Perigonia lusca* and *Enyo ocypete*, commonly arrive at the Santa Rosa lights during the night.

Sphingids conspicuously display lunar phobia as measured by numbers taken in light traps through the lunar cycle (Bowden and Church 1973, Robertson 1977, Harling 1968). Santa Rosa sphingids are not exceptions. However, I suspect that the effect is more due to the moon obliterating the attraction or arrival effects of the artificial light than through cessation of sphingid activity. Certainly some species of Santa Rosa sphingids can be observed to forage at flowers under a full moon (e.g., those mentioned above visiting *Stachytarpheta frantzii*). If it is eventually shown that sphingids curtail flight activity during lunar illumination, they will then be quite different from the saturniids at Santa Rosa. While there is a noticeable decline in numbers of saturniids arriving at lights during lunar illumination, no such decline appears in catches of males at traps baited with calling females, even if she is calling with a full moon nearly overhead. Likewise, a female saturniid with only a few days to live could hardly cease her oviposition activities to wait days for a substantial reduction in lunar illumination; the female sphingid, however, does have this option.

There is mounting evidence that Costa Rican sphingids regularly migrate tens of kilometres (W. Haber, personal communication); there are no suggestions of migratory behaviour by saturniids, though waif male saturniids do occasionally appear far from their birthplace (seven individuals of four species in six light-years at Santa Rosa). It is commonplace for large numbers of sphingid individuals of a few species to be taken at a very exposed light far from anything that approximates breeding habitat for these species. For example, on 4 December 1983, at a 1800 m elevation pass in the mountains between the Pacific coastal lowlands of Costa Rica and the Atlantic rainforested coastal lowlands, a light such as the Santa Rosa lights, placed on a prominent grassy knoll, attracted a minimum of 403 males and 741 females of 12 sphingid species. All 12 were species that breed at Santa Rosa and not at the elevation of the light, and all were species that disappear from the Santa Rosa lights during the dry season but occur throughout the year in the Atlantic rainforests of Costa Rica. The same light also attracted ten males and one female of four species that breed in the wet forests at the collecting site. It seems reasonable to hypothesize that these lowland sphingids arrived at the light in the pass not because they just happened to fly haphazardly through the zone of direct attraction, but rather because when migrating, they use a bright star as an orientation landmark or as a direct beacon; the artificial light was simply a

star mimic, and one that would have been of no interest to these individuals in the sky at Santa Rosa or other Pacific lowland site. In the 1800 m pass, my light was probably an exceptional star mimic since there were heavy clouds and occasional drizzle. This aspect of migratory arrival at lights is simply missing from saturniid biology, but can be an important aspect of sphingid arrival at Santa Rosa lights both when migrants are incoming and initiating a journey.

Sphingid generations at Santa Rosa are initially quite asynchronous due to variable responses to cues to break pupal dormancy. They become even more asynchronous as the rainy season progresses due to long-lived ovipositing adults and variable pupal durations. While there should be a few newly eclosed naive adults (and exploring experienced adults) available to arrive at lights on any rainy season night, the number of adults arriving should be a very poor estimator of the total numbers present. When migrants arrive (or leave), they may arrive at the lights in numbers proportional to their true numbers, but their rapid subsequent decline in numbers at the light says little or nothing about their actual density in the habitat. This suggests that in contrast with saturniids, census of sphingids at lights (e.g., Wolda 1980, Owen 1969) is only partly understandable without detailed corroborative data from other sources such as larval density. Light traps are very convenient, but like sweep samples, are highly suspect census devices. Certainly the presence of male or female sphingids, even if regular in occurrence, cannot be used as firm proof that there is a breeding population in the vicinity of the light. On the other hand, when female saturniids occur at a light there is very likely to be a breeding population in the immediate vicinity while male saturniids are less good indicators unless they occur in large numbers on a regular basis.

In closing this section I wish to leave the reader with the caricature that saturniid males, in their single-minded pursuit of female pheromone plumes, are fairly stupid flying machines that can be behaviourally derailed by a light. They have neither the time for extensive learning of the habitat, orientation needs that change in space and seasonal time, nor resources in a fixed pattern that can be learned. Sphingids, on the other hand, must possess a fairly complex learning capacity such that each individual can finely tune itself to its local nightly harvest of resources. While the adult is still young it is susceptible to false landmarks such as an artificial light, but with advancing age and experience becomes relatively immune as it settles into a routine of resource harvest. However, even an experienced sphingid may again become susceptible to capture at light when important traditional cues are obliterated such as when there is a dense fog or heavy drizzle, which should generate both the blackest night and the most odour-free atmosphere. Likewise, migration and exploration off established foraging routes may render the experienced sphingid again dependent on lights. However, both drizzle and long migration flights may cause sustained wing wear, rendering age evaluations somewhat problematical (R. Peigler, personal communication).

Why are adult saturniids so polymorphic?

Figs. 1–4 will acquaint the reader with two of the three ways that adult Santa Rosa saturniids are conspicuously more polymorphic than are adult sphingids: between sexes, among species, within a sex. First, the males can be easily distinguished from their mates by colour, size and/or wing shape (e.g., compare Fig. 1.1 with 1.2–1.3, 1.4 with 1.5–1.6, 2.18 with 2.19, 2.20 with 2.21). The sexes can be distinguished in flight, if illuminated, while sitting at the light among other moths, and while at rest in foliage. Sphingids, on the other hand, usually require close scrutiny to distinguish the sexes even when spread and well illuminated; *Amplifyterus ypsilon* and *Protambulyx strigilis* are perhaps the most easily sexed of the sphingids in Figs. 3–4, and only two other Santa Rosa sphingids are slightly more dimorphic in wing size (*Pseudosphinx tetrio* and *Madoryx oclus*, both with very heavy-bodied and broader-winged females). Four species of Santa Rosa sphingids can be sexed by small differences in the variegated bark-like patterns on their wings. Sphingid sexes can be distinguished with practice by noting fine differences in the curvature of wing margins, wing maculation, body thickness, etc. However, as a group, the Santa Rosa sphingids are in general aspect much more similar between the sexes than are Santa Rosa saturniids. These differences are not a unique local phenomenon, as saturniid sexual dimorphism is prominent in other parts of the world (e.g., Tams 1924, Peigler 1976a, 1983, Ferguson 1972) while the most dimorphic extra-tropical sphingid appears to be the North American poplar sphinx, which does not feed as an adult.

Second, saturniids vary strongly among the species in wing shape, while sphingids have quite similar shapes among the species. It is easy to draw a silhouette that will almost exactly cover each sphingid in Figs. 3–4 just by shrinking or expanding; no such universal shape can be drawn for the saturniids in Figs. 1–2. This is true whether the silhouette is made for one sex or for all individuals. Adding the remainder of the Santa Rosa saturniid and sphingid species to Figs. 1–4 would not invalidate the generalization.

The third form of polymorphism is visible in Figs. 1–2 only in *Adeloneivaia isara*, *Copaxa moinieri*, *Rothschildia lebeau*, and *Hylesia lineata*. However, 17 of the 30 saturniids that breed in Santa Rosa have two to four colour morphs within the adults of one or both sexes. Among adult Santa Rosa sphingids there are none. In the world fauna of saturniids, intra-sex colour polymorphisms are commonplace (e.g., Peigler 1976a), while the poplar sphinx mentioned above is the only sphingid example known to me. There are, however, examples of sphingids that vary geographically in colour, such as the (apparently) non-migratory *Amplifyterus gannascus* at Santa Rosa which are lighter in colour (and smaller) than their Costa Rican rainforest counterparts (W. Haber, personal communication).

There is something quite different about the biology of wing function of saturniids and that of sphingids. I hypothesize that the basic difference is due to saturniids not feeding as adults, with various degrees of directness in the causality. The effect of this difference should be more pronounced in a

tropical dry or strongly seasonal habitat such as Santa Rosa than in lowland tropical rainforests such as those found in other parts of Costa Rica. Whether the trait of non-feeding as an adult should be viewed as a cause or consequence of the saturniid life style will be discussed later.

Sexual dimorphism. A male saturniid is a flying machine specialized primarily for one activity, finding females – fast. And he does it while carrying only the weight of the machine and the fuel and water needed for five to 10 days survival. His female is a flying machine specialized primarily for a very different activity – locating host plants and laying eggs. She does it carrying not only the weight of the flying machine and its fuel, but also an egg load weighing more than half her initial body weight and diminishing rapidly as her potential fitness declines through oviposition and wing wear. A male saturniid wins by getting to females fast over long distances; a few seconds of flight time can make the difference between expressing zero or one fifth of the male's potential fitness. There is no second place prize money. A female saturniid wins by finding a few large host plants and getting rid of her eggs quickly, but she can afford more short term delay, at least within a night. Yes, both sexes avoid predators and desiccation, but each sex does this in different, even if overlapping, microhabitats. Such different functions should select for quite different flying machines, and appear to have done so.

Male sphingids also search for females. However, they also regularly hover in front of flowers to harvest fuel and water with their long proboscises. Female sphingids also search for oviposition sites. However, like the males, they nightly hover in front of flowers to drink. In short, male and female sphingids have a major kind of activity in common. If they belong to a migratory species, they have even a second major kind of activity in common. Such communality of flight activity should be a major barrier to the evolution of quite different morphological phenotypes, even if other aspects of the life history are selecting for them.

What aspects of saturniid biology may lead to more exaggeration of the male/female differences than is found in sphingids (remaining within the confines of an intra-specific comparison)? The male saturniid has its one and only harvestable resource available for only that (short) time when females of its species are calling with pheromones; its flight behaviour and aerial predator avoidance should be evolutionarily engineered to match primarily the challenges that occur during that one period (it is unknown how much flight occurs during the post-sunset dispersal flight, but I suspect it to be only a few minutes). Female saturniids also have a narrow activity period, but it is at a different time of night than the males fly (except for those few species that both mate and oviposit during the first few hours of the night). A pair of sphingids, however, probably has flower resources available throughout the night and therefore may be experiencing the same challenges from predators and weather. If the species migrates, both sexes probably migrate and are shaped by the same selective pressures for migration ability.

Assuming that a male saturniid is competitively functional for only five

nights, it can mate only a maximum of five times and its potential fitness must steadily decline with age (assuming that it stays in copula all night if a mate is found, as is true for at least 66 per cent of the Santa Rosa saturniids). Fast accurate flight irrespective of obstruction is paramount. Loss of 20 per cent of a mate's fitness may occur by using a few seconds to carefully negotiate a vine tangle around a female rather than by blasting through it irrespective of wing damage, or by hesitating to examine a potential predator near the calling female. For the saturniid female, however, wing-tattering speed and oblivion to obstructions may be less important than is accuracy of finding a few large hosts each night. Whether she finds a host at 1900 or 1910 hours may not be very critical. Her ability to flutter (helicopter) through the foliage while bearing several grams of eggs is paramount. She even hangs on the foliage with (sometimes) lightly beating wings while ovipositing; sphingid females oviposit in hovering flight that is just slightly supported by extended legs in contact with the foliage. If a saturniid's aerial caution or clumsiness slows her oviposition rate, it need not lower her potential fitness if she is not taken by a predator before the next oviposition bout and/or if she can compensate by laying more eggs in the next tree crown.

The male sphingid, however, uses its wings for weeks to months for resource harvesting as well as mate location. Care of the wings and caution in flying can increase potential fitness through lengthened life span and greater flight competence later in that life span. The female sphingid is subject to the same suite of selective pressures, and even uses her wings as does the male when she is hovering for oviposition and evaluation of oviposition sites.

Since saturniids have a fixed and very short period in which to express their potential fitness, I expect selection to result in bizarre solutions to how to do it fast. Such solutions are less likely to be evolutionarily invented by sphingids with their longer time to act and therefore more ways to integrate compensatory and antagonistic activities. For example, *Hylesia lineata* (Fig. 2.7–2.10) has carried its speed of oviposition to the extreme of putting all of its eggs in one basket (a single ball of 100–450 eggs covered with an elaborate felt pad constructed of interlocking abdominal hairs, Janzen 1984a). Its potential fitness goes from high and nearly constant (the adult female is well protected from vertebrate predators by urticating hairs) to zero in one act; the flying machine has only to function under the stress of a full load, and never has to function at a light body weight of a male. A second example is that a *Syssphinx molina* female seems to have a probability of near unity of getting a mate the night she ecloses and a host tree the following night; she often begins to lay sterile eggs on the night of eclosion if not quite literally plugged by a male, and she lays as many as two-thirds of her (sterile or fertile) 200–400 eggs the following night even if confined to a plastic bag with no host plant odours. Such oviposition behaviour strongly selects for, or could only evolve in the presence of, highly reliable mating and a female phenotype associated with rapid location of a few host plants (such as the huge crowns of *Pithecellobium saman*, the primary *S. molina* hosts at Santa Rosa). Such behaviour is also

only compatible with the traits of a small subset of the Santa Rosa plants that might be physiologically suitable pabulum for *S. molina* caterpillars (assuming them to be monophagous or narrowly oligophagous). The male *S. molina* is, on the other hand, confronted with the task of courting widely over the relatively dry kinds of open and low forest where *S. molina* is common in the Neotropics. *S. molina* seems to require little more than open pastureland dotted with huge adult *P. saman* to stay in the game in the face of human habitat destruction.

Perhaps the most extreme dichotomy of selective regimes acting on conspecific male and female saturniids is absent from Santa Rosa – that of diurnal males in pursuit of calling (stationary) females and nocturnal ovipositing (flying) females. Such pairs are well known in extra-tropical regions. Their males have colours and wing shapes quite distinct from those of their females; the phenomenon is apparently generated by inter-specific competition among congeners for a time of day (or night) free of allospecific males (e.g., Toliver *et al.* 1979, Brown 1972, Peigler 1976a, 1981, Ferguson 1972). While diurnal saturniids are abundant extra-tropically, all but one of the few Neotropical ones are in high and cold and/or dry habitats (R. Peigler, C. Lemaire, personal communication). The exceptional deep tropical diurnal saturniid is *Automeris phrynon*, whose males arrive like high-speed bright yellow and brown butterflies in full morning daylight to the calling females in Costa Rican rainforest (Marquis 1984). The females fly to oviposit at night, come to lights occasionally (the males never do), and weigh four to five times as much as the males at the time of eclosion. *A. phrynon* is the only diurnal *Automeris* and the most sexually dimorphic. Reminiscent of the postulated cause of the diurnality (and hence strong sexual polymorphism) of the saturniid *Callosamia* in the eastern US, *A. phrynon* co-occurs with at least 10 species of *Automeris* in Costa Rican rainforest. Competition for pheromonally clean airspace must be severe, especially since there is a suggestion that all *Automeris* males are at least physiologically capable of reacting to each other's allospecific females' pheromones (Priesner 1968).

In fact, perhaps the most puzzling aspect of saturniids is that the males and females resemble each other at all. Intra-specific phylogenetic inertia is the likely dominant cause, but that jargon phrase for being stranded on the top of a steep-sided adaptive peak does not disclose the actual processes. It is likewise not a very satisfying reply when, even within the wild population of a Santa Rosa saturniid, there can be functional males weighing as little as 10 per cent of the weight of a newly eclosed conspecific female. For example, the ordinary-sized *Othorene purpurascens* male in Fig. 1.5 weighed 1.02 g while his wild-caught male congener in Fig. 1.6 weighed 0.23 g but was functional if I may infer from controlled matings in other Santa Rosa species such as *Rothschildia lebeau*. The same applies to the contrasting *R. lebeau* males in Figs. 1.10 and 1.11. It might also be argued that the male saturniid rests in the same ecologically similar diurnal habitat as does the female (but see below under intra-sex polymorphism) and therefore if they both start on the same cryptic adaptive peak, they are likely to remain there. Likewise at night, while he flies at different speeds

and with a different goal than she does, they both fly through the same general habitat at least part of the time.

Yet why does he not live longer than she does (longevity trials at Santa Rosa give no hint of this) by accumulating as much resource while a caterpillar as she does? He would, however, then be a slower (heavier) flier and perhaps be more awkward. Additionally, since female saturniids are often very pulsed in their seasonal availability, greater male longevity might be of less value than it would be to a moth with a more even temporal distribution of receptive females. An answer to the question of why saturniids are not more dissimilar between the sexes will require more knowledge of their biology than is at hand.

Interspecific variation. No Santa Rosa saturniid species feeds as an adult or migrates; the freedom from these constraints allows species, as it does sexes of one species, to go its own evolutionary way according to differences in flight demands of the habitats occupied, oviposition host spacings and physical structures, predator avoidance, diurnal roosting sites, etc. This may even be at the root of why saturniids are sufficiently different among species that there has been considerable argument over whether they should be split into several families and why saturniids have so many distinctive subfamilies (as compared with sphingids). A pair of saturniid species of recent mutual derivation may diverge strongly if in quite different habitats while a pair of sphingids with the same evolutionary proximity in time and in equally dissimilar habitats may remain morphologically much more similar than will the saturniids for two reasons. First, the sphingid species will have hovering flight and (perhaps) migratory flight in common. Second, with their long adult life spans and ability to gather food and water as adults, they can have more kinds of physiological, ecological and behavioural solutions to dissimilar habitat challenges, instead of expressing solutions in readily visible wing traits. In short, a set of 30 species of similar-appearing sphingids may have as divergent biologies as do 30 species of quite different-appearing saturniids in the same habitat. However, it is not clear that one can argue that a major constraint such as a fixed wing shape in an aerial organism can result in fewer solution options when the remainder of the life cycle has many other facets that may be stretched in compensation. For example, sphingids as a group can make use of many more species, life forms, specific ages, and abundances of oviposition sites than can adult saturniids, if for no other reason than that they have the adult time, brains and flight agility to search them out.

It is easy to conclude that the wing shape so characteristic of adult sphingids is somehow one of the 'right' ones for fast and accurate hovering flight (and in this, conspicuously convergent on that of hummingbirds, Casey 1976). However, I cannot be firmly specific about the function of the various interspecifically different wing shapes of the Santa Rosa saturniids. A few guesses may be illuminating, however. Of the five arsenurine saturniids at Santa Rosa, the males of three of them fly unharried, and when escaping, as does the male of *Titaea tamerlan* (Fig. 2.19) – with a fast

and flapping wing beat, erratic trajectory when threatened, and high speed. *Arsenura armida* males remain immobile and display their yellow body ornaments when attacked, have the most rounded and tailless wings, and fly straight with a hemileucine-like very fast wing beat. The fifth arsenurine, *Copiopteryx semiramis* (Fig. 2.11), flies slowly to fast in a nearly straight trajectory with a moderately rapid wing beat, and the long tails stream out behind with the tip of each tracing a five to 10 cm diameter circle in a plane at right angles to the trajectory of the moth. I suspect that the tails render this moth, the smallest (lightest) of the arsenurine saturniids at Santa Rosa, the largest saturniid in the Park in the sonar imagery of a bat.

The ceratocampine saturniid males (Figs. 1.5, 1.6, 1.8, 2.4–2.6, 2.13, 2.14, 2.15, 2.17) are the fastest-flying saturniids in the Park. I cannot distinguish individual wing beats in flight; ceratocampine males arrive at a light at about the speed of a thrown rock, and as mentioned earlier, a male *Eacles imperialis* was clocked with a speedometer at 60 km/hr. They have the longest and narrowest (most sphingid-like) wings, are disproportionately species-rich in dry and open sites like Santa Rosa, have arid-land plants primarily as larval hosts (e.g., Table 3), and are easily caricatured as specialists at flying long distances in clear airspace (as mentioned earlier for the ceratocampine *Syssphinx molina*).

Hemileucine saturniids (Figs. 1.12, 2.7–2.10, 2.20–2.21) tend toward more rounded wings, fly with a very buzzing and controlled flight (though erratic trajectory if fleeing), moderate forward speed, and extreme agility in and around dense foliage at high speed. I cannot help but note that practically all the increase in saturniid species richness in moving from Santa Rosa's dry forests to the wetter lowlands of Costa Rica is due to hemileucines and/or *Copaxa* spp. (e.g., Fig. 1.1–1.3), which very much resemble a hemileucine when in flight. However, this observation is confounded by the observation that hemileucine caterpillars, being urticating, are the best-protected against vertebrate predators and are the most polyphagous of the saturniid caterpillars. To proceed further and more authoritatively in these directions will require considerably more natural history information on neotropical moths than we have at present.

Intra-sex polymorphisms. While the Santa Rosa adult sphingids display no within-sex polymorphism, over half of the Santa Rosa saturniids do so. The saturniid polymorphism is of two types, with compatible and overlapping causes. First, there is a conspicuous seasonal polymorphism, whereby light-coloured morphs predominate during dry spells during the rainy season and in the dry weather around the beginning of the rainy season. *Adeloneivaia isara*, *Othorene verana* and *O. purpurascens*, and *Rothschildia lebeau* display the trait most clearly. Greater than 95 per cent of any large sample of newly enclosed *R. lebeau* taken at lights or with virgin female-baited traps during the week before the rains start to a week after (late April to late May) range from nearly orange to a bright rusty red in background colour (Fig. 1.9). During a month of rainy weather, better than 80 per cent range from dark chocolate brown to dark rusty brown

(Fig. 1.10). Both sexes display the changes in about equal proportion, but the females achieve the lightest colours and the males the blackest. *Adeloneivaia isara* displays the same seasonal change in the proportions of the colour morphs in Fig. 2.1–2.6. I have postulated (Janzen 1984c) that these highly edible moths are basically mimics of hanging dead leaves during daylight hours and have been selected to resemble a light-coloured dry dead leaf during dry weather and a dark wet mouldy leaf during rainy weather. The colour differences are cued or caused by the temperatures of the pupal environment. It is tempting to suggest that at least one reason why Santa Rosa sphingid do not have this kind of seasonal polymorphism is that a sphingid is designed to live for enough weeks that its colours will have to serve in long periods of both dry and wet weather.

Second, there is a type of polymorphism whereby the males have two to four different but variously intergrading colour morphs, and the females no more than two. Here there is no apparent relationship of season to preponderance of any one colour, though all colour morphs for a particular species are not equally abundant. *Syssphinx quadrilineata*, *Automeris zugana*, *Hylesia lineata* (Fig. 2.8–2.10), *Copaxa moinieri* (Fig. 1.2–1.3), *Caio championi* and *Titaea tamerlan* all display this kind of aseasonal polymorphism. The seasonal polymorphisms can be added back into the system at this point, since all of their morphs are present in any large sample of adults.

I suspect that the primary cause of the aseasonal saturniid polymorphism at Santa Rosa is the large number of adults that occur at periodic and aperiodic intervals, due to seasonal cueing of adult eclosion, synchronized timing of larval and pupal duration of subsequent generations within the season, and occasional population highs. Such pulses of high density of edible adults quite probably result in rapid formation of search images by individual vertebrate predators for whatever morph they first encounter in abundance, resulting in selective favouring of the other morph. The peaks can be enormous. During a population high of *Hylesia lineata* as many as several hundred males came to a single light in one night (Janzen 1984a); in a different year, 174 male *Automeris zugana* arrived at one light one night. On 23 May 1982, 19 female *Caio championi* arrived at a single light in response to a uniformly perceived start of the rainy season. Sphingids at Santa Rosa are more uniform in their abundance than are saturniids, or at least less commonly reach such spectacular peaks in density. When there has been an exceptional density of sphingids (e.g., *Aellopos titan* defoliating *Randia*, Janzen 1984b), the adults leave the habitat immediately after eclosion. However, there could well be other aspects of sphingid biology that nullify any selection that there might be for aseasonal polymorphism in sphingids.

Habitat gradients. Several changes pertinent to the biology of Costa Rican saturniid polymorphisms are encountered when moving from the dry seasonal forests of Santa Rosa to the more uniformly wet low elevation rainforests of Costa Rica. First, the saturniid species in common between the two sites (94 per cent of the Santa Rosa saturniids) are invariably

monomorphic at the rainforest sites and the morph is as dark or darker than is the Santa Rosa darkest morph. This generalization applies to all the different patterns of adult polymorphisms mentioned above and to all the moths mentioned except *Adeloneivaia isara*, which in Costa Rica occurs only in dry forests. It is striking that the other three species of Costa Rican *Adeloneivaia* (*A. jason*, *A. boisduvalii*, *A. subangulata*) are all monomorphic and are all rainforest species (in South America, where these species occur in both wet and dry sites, there are dry season light-coloured morphs, C. Lemaire, personal communication). At least part of the answer to why Santa Rosa saturniids are seasonally polymorphic rather than simply generally of a lighter colour than their rainforest relatives is that the dry forest is in fact seasonally as dark as is the rainforest and the dry forest also contains strips and islands of evergreen forest.

Second, the drier the site, the more pulsed will be the density of saturniid adults because the more accurately and thoroughly can be perceived the weather cues. A given annual number of adults at a dry site will present better conditions for selection for colour polymorphisms than will the same number of eclosions spread throughout the year at a rainforest site. The same effect is generated by the more frequent saturniid population highs at dry sites than at rainforest sites. The very low density between successive population highs should not select against extant polymorphisms (assuming all to be equally cryptic), but the conditions during the peak are excellent for selection for adult polymorphisms in non-migratory species.

Wings have other uses. While my emphasis has been on wings as flight devices and the major cryptic structure when sessile, there are other selective pressures on wings that may lead to differences between saturniids and sphingids. First, sphingids are singularly unimaginative in their initial dash for freedom when approached or fumbled by a vertebrate predator. Santa Rosa diurnal temperatures are generally warm enough (27–32 C) for the moth to attempt to fly away with rapid wing beats, becoming more rapid as the flight muscles warm up. In contrast, Santa Rosa saturniids are highly variable in diurnal escape behaviour and many of the ways relate to wing shape and colour. Male *Rothschildia lebeau*, *Copaxa moinieri*, *Caio championi* and *Titaea tamerlan* launch into instant fast and erratic flight, achieving this with relatively few beats of their large wings. Fleeing males then come to an abrupt halt on contact with vegetation, once again achieving the hanging dead leaf pose, complete with a faint and temporary side-to-side oscillation like that of a breeze-disturbed leaf. The females of these species, however, respond to a touch by locking their wings in a nearly spread position and letting go of the substrate. The appearance and dynamics of the gliding and falling moth matches exactly that of a large leaf falling generally downward while side-slipping such as to trace out a zig-zag trajectory. Landing on the litter with the upper surface of the wings upward, or hanging up as she passes through a tangle of vines, the moth is an excellent behavioural mimic of a falling leaf (whose colour pattern it also possesses). Both sexes of *Eacles imperialis* also fall this way,

but after a few minutes of invisibly warming up its flight muscles, the male launches into extremely fast flight up through the general forest canopy. When the males of *Citheronia* become motionless (see below) they often let go of the substrate and fall with no attempted flight; however, the stereotyped posture, the heavy body attached to the four tightly appressed wings (erect, over the back), creates a device that spins in the air and looks exactly like a large falling samara. Selection for wings and body weights that function in escapes such as these can be partly responsible for saturniid sexual dimorphisms, especially since the female has to weigh much more than does the male because all her egg resources have to be with her from the beginning.

Rather than flee from vertebrate predators, at least 50 per cent of the Santa Rosa saturniids raise the wings above the body and display a ringed (orange, yellow, red, black) abdomen and/or large eye mimics on the hind wings when molested (and see Blest 1957a, 1957b, 1960, Gardiner 1967, for description and ethological analysis of this behaviour). Except for two species of *Automeris* and one *Hylesia*, there is a striking lack of colour and aspect polymorphism within each of these aposematic/mimetic species. Why *Automeris* (and *Hylesia lineata*, which looks like a little *Automeris*) should differ is not evident, unless perhaps it is more edible than the others.

There is still the puzzle of why female saturniids are generally less polymorphic than are the males, especially in intra-sexual aseasonal polymorphism. It could be caused by the males being subject to more kinds of predators than are the females; some predators should favour a different pair of morphs than would others, through the particular way they form search images. Additionally, females may well roost in a more restricted subset of the habitat sub-sites than do the males; certainly all females spend their first day (the most important one) in the shadiest part of the habitat only a few tens of centimetres above the ground and often in copula. Females may also roost in the vicinity of the crowns of their ovipositional host plants, while males are likely to roost in a greater variety of sites since in their search for calling females they will have to cross virtually all habitat types and move through all heights of vegetation.

Why do saturniid and sphingid caterpillars eat different plants?

Saturniid and sphingid caterpillars are the big ones at Santa Rosa just as they are in other parts of the world. A last instar female *Eacles imperialis* caterpillar weighs 25–30 g, as does a last instar *Eumorpha anchemola* or *Neococytius cluentis*. Medium-sized saturniids and sphingids have caterpillars that are as heavy before they pupate as are those of the largest noctuids, notodontids, megalopygids, etc. Saturniid and sphingid caterpillars have the same general goal – eat leaves in such a manner as to grow rapidly large enough to pupate, without being found by a carnivore. One might therefore expect the caterpillars of each family collectively to consume about the same subset of the vegetation, the one that is best for this goal. However, for the most part each group does not consume the same plant

species, combinations of plant species, or life forms (Tables 3–4). This difference occurs with no hint of character displacement over larval food plants, either as evidenced with outcomes or as indicated by the existence of inter-specific interfaces appropriate for its evolution (though there are many indirect and inconspicuous ways that saturniid and sphingid caterpillars can influence each other, such as by sharing parasitoids). The larval food plant patterns suggest to me that saturniid and sphingid caterpillars have different goals and that their different adult biologies may dictate different optima for their caterpillars (and vice versa).

I have already briefly caricatured the caterpillars of Santa Rosa saturniids and sphingids in the introduction and have mentioned them in the previous two sections. Saturniid caterpillars are slower-growing and less cryptic with a more fixed development time on apparently lower quality food selected from a larger subset of the available plant species and families but a smaller subset of the life forms, than is the case with sphingids. Not only do the saturniids feed on a distinctive and different set of plant families than do sphingids, but Santa Rosa saturniids (especially the hemileucines) display a greater degree of polyphagy than do the sphingids. In general at Santa Rosa, saturniid caterpillars eat phenol-rich and/or aromatic foliage of big trees and/or smaller perennials (Table 3); sphingid caterpillars eat foliage that is traditionally viewed as rich in toxic small molecules, almost entirely in the Solanaceae, Apocynaceae, Asclepiadaceae, Euphorbiaceae, Bignoniaceae, Flacourtiaceae, Rubiaceae, Verbenaceae, Labiatae, Convolvulaceae, Moraceae, Vitaceae, Boraginaceae, Dilleniaceae, Anacardiaceae and Lauraceae (Table 4). The saturniids also feed on foliage significantly less water-rich than do the sphingids at Santa Rosa (Janzen and Waterman 1984).

There are therefore at least two ways to grow a big caterpillar that eats leaf blades. I have not the space or expertise to discuss these two ways for the world fauna of saturniids and sphingids but in closing will briefly mention some ways that the Santa Rosa fauna seems to depart from that of other tropical areas. Below I will focus on what seem to be some of the major aspects of saturniid and sphingid biology that have led their caterpillars to feed on different subsets of plants: amount of time available for oviposition, compatibility of crypticity with polyphagy, physiology of fast caterpillar development, and what is wrong with small life forms as host plants.

How to oviposit in a short time. There are at least three ways that a saturniid may get her eggs to the right places in a short time: have a conspicuous host, lay eggs in large batches, and/or have polyphagous caterpillars. First, she may be a specialist at locating a single plant species that is, from her viewpoint, conspicuous because its density is high, it is very odoriferous, and/or it is very large. There are a number of consequences of following this route. For such a monophagous moth species, there is no selection on the larvae to be either capable of digesting other species of plants or cryptic on them. There should be few impediments to the caterpillar evolving digestive abilities as efficient (or

thorough) as are biochemically possible and also evolving to be quite cryptic on the host. Additionally, the plant species that are initially evolutionarily chosen by the moth may well be those that are especially digestible to a saturniid by virtue of being both low in digestion inhibitors and toxins (e.g., *Bombacopsis quinatum*, the sole local host of three of the five monophagous Santa Rosa arsenurines, has no indication of foliar toxins and has low foliar phenolics (Janzen and Waterman 1984); *Manilkara chicle*, the host of *Copiopteryx semiramis*, has latex-rich foliage and would therefore appear to group with the many latex-rich sphingid host plants – however, its latex is so innocuous that it was the original base for chewing gum). Similarly, plants offering exceptional freedom from carnivores should be evolutionarily chosen by such saturniids (e.g., the ant-acacias as the sole larval hosts of *Syssphinx mexicana*; the crowns of large trees).

The Santa Rosa saturniids contain a number of examples of saturniid-host pairs that seem to conform to the above generalizations. *Copaxa moinieri* is an exceptional saturniine saturniid in having only one host, which is also a small plant (and furthermore, the caterpillar is restricted to saplings and the lower parts of large adult plants). However, *Ocotea veraguensis* is an abundant understory shrub and like other Lauraceae (e.g., bay leaves) it has very odoriferous foliage. Furthermore, the large genus *Copaxa* seems to be a lauraceous specialist (Janzen 1984d) and if there were other species of Lauraceae at Santa Rosa, *C. moinieri* would likely have a longer host list (it is striking that several species of *Copaxa* can, however, be reared on *Crateagus* and *Salix* in Europe, C. Lemaire, personal communication). Only one Santa Rosa saturniid—*Dysdaemonia boreas* – is restricted (apparently, at least) to a very rare tree – *Ceiba pentandra*. However, the tree is huge and the moth is the rarest breeding saturniid in the Park. *C. pentandra* is (and especially, was) moderately common just outside the Park and throughout its range from Mexico to Brazil, which is also the range of *D. boreas* (Lemaire 1980). It is a fair guess that *D. boreas* would not be a member of the breeding fauna of Santa Rosa saturniids if the population had to persist on only the three known adult *C. pentandra* in the Park.

Second, a female may place her eggs in large batches, thereby substantially reducing the number of actual oviposition sites she has to find (and increasing the time that she has available to search for them). *Hylesia lineata*, putting all of her clutch in one felt-covered ball (Janzen 1984a) is the extreme form of this trait. Whether *H. lineata* can retain its position as the most polyphagous of the Santa Rosa saturniids remains to be seen as more records accumulate for *Automeris rubrescens*, *A. zugana*, and *Periphoba arcaei*. The other seven Santa Rosa hemileucines for which oviposition is known lay batches of 30–150 eggs (about 0.1–0.5 of a female's fecundity per batch). Such oviposition behaviour selects for either ovipositing in very large tree crowns (e.g., *Arsenura armida* oviposits about half its egg load in one place in a huge *Bombacopsis quinatum* crown), being a small caterpillar in small tree crowns (e.g., *Hylesia lineata* on any of its numerous hosts), and/or being so polyphagous that once all

the food has been eaten off the plant, the caterpillars can move on to other species (e.g., *Automeris rubrescens*, *A. io*, *A. zugana*, *Periphoba arcaei*, *Hylesia lineata*, *H. dalinaa*). Oviposition in batches also sets the stage for the evolution of caterpillar group defences (e.g., as shown by *Hylesia*, Hogue 1972, Janzen 1984a) and feeding behaviour, and need not result in defoliation of individual host plants if there is very heavy carnivory of the young caterpillars. Looked at the other way around, group oviposition can be viewed as having been selected for by the various advantages of group living (e.g., larger aposematic displays when young), but the above constraints and advantages apply anyway.

Third, she may oviposit on any one of many host species. While this means that she can find a host plant more quickly, she must also either have a number of different cueing systems or the members of her multi-species oviposition list must have cues in common that enable her to distinguish them from the hundreds of species of plants on which the most polyphagous Santa Rosa saturniids are never found (or some combination of these two traits). The caterpillars must not only be able to develop on a greater variety of diet and chemical defence types, but also be able to withstand the carnivory regimes of those host plants with little aid from detailed crypticity or a short larval development time. It is possible that such a moth is acting like a plant – it hits some good development sites (host plants) with its offspring by distributing them in a pattern that has the intrinsic property that many are certain to die. When a female *Automeris io* places 30 eggs on a *Rhynchosia calycosa* vine (a very small plant), its evolutionary past is assuming that somewhere in the vicinity of that plant there are sufficiently edible other plants to sustain some of the 30 caterpillars. It is in the polyphagous species with many oviposition sites that I expect the longest development times and the greatest variation in intra-specific development time. At Santa Rosa, *Automeris rubrescens*, *A. io*, *A. zugana*, *Periphoba arcaei*, and *Hylesia lineata* are the most involved in this kind of biology. They are conspicuous in being able to starve for as much as four to six days with only a slowing in weight gain, being able to (usually) change hosts at any instar (among the hosts on which that species feeds), being urticating and aposematic, varying in development time as much as 2.5-fold within a clutch of siblings feeding on different host plants (but being similar in body weight at pupation), and being able to eat a large yet distinctly circumscribed set of species (e.g., Table 3).

Hemileucine caterpillars have a peculiar behavioural trait that relates strongly to their polyphagy. When attacked, they often let go of the substrate and fall. Being polyphagous, even if oligophagous, then they are more likely to be able to relocate at least one edible host than if they were monophagous. All the non-hemileucines at Santa Rosa will not voluntarily release their hold on the substrate even if being ripped to pieces by a wasp or bird (as is generally the case with sphingids as well). This behavioural trait should also contribute directly to the frequency with which the collector encounters hemileucine caterpillars on all their potential hosts and suggests that the long host list of a polyphagous hemileucine need not

imply a long list of species suitable for oviposition (however, I have never found a batch of hemileucine eggs on the foliage of a species not eaten by that hemileucine).

By virtue of their short time available for oviposition, saturniids seem to be preadapted for continuous ecological, and hence evolutionary, sampling of the host plant offerings in a habitat. SpHINGIDS appear to be the opposite since the unlucky female spHINGID should wait until the next night or even leave the habitat to search for a good oviposition site. Since saturniid females lay all their eggs before dying, even in the laboratory with no host plants available, and since in the laboratory the absence of a host plant only deters saturniids from ovipositing for a few hours or days (if at all), I suspect that in nature a female saturniid must often place all or part of her night's eggs on atypical hosts. Yet the records in Table 3 include all wild living saturniid host records for over 800 different accessions over six years (a clutch of gregarious caterpillars is recorded as one accession). The stenophagy portrayed by the non-hemileucines in Table 3 suggests that even though they feed on many families of large plants, a given saturniid species is still rather tightly bound to its particular host(s) in a given habitat.

Incompatibility of crypticity with long or diverse host lists. While I have already alluded to the incompatibility of crypticity and polyphagy at numerous places, it deserves explicit mention. Non-cryptic defences, such as extreme urtication, should be strongly selected for as companion traits to polyphagy. Polyphages should often find themselves on quite different leaf shapes, colours, sun exposures, etc., than those experienced by their siblings and conspecifics. Additionally, they may have to cross non-leafy surfaces in search of new host plants. Finally, by growing slowly, they are exposed to carnivores for a maximum time. Viewed the other way around, a caterpillar with a very effective defence against both vertebrate and invertebrate carnivores might well be able to eat almost anything, albeit while growing at some excruciatingly slow rate on certain of these hosts.

There is an important but easily overlooked complexity in the relationship between crypticity and duration of the larval period. If a caterpillar relies totally on crypticity for its defence, the more days that it is a caterpillar, the more likely it is to be found while a caterpillar. If a caterpillar can rely totally on a violent and self-evident personal defence such as urtication, additional days of development will not only mean no additional risk, but may even lower the average daily risk of carnivory if the carnivores are local ones that learn about the presence of a particular individual caterpillar. The above dichotomy is blurred by the existence of certain vertebrates that can eat well-protected caterpillars, and by the fact that what deters a vertebrate may have no effect on a parasitoid fly or wasp. However, risk of being taken by a parasitoid may also not necessarily increase with larval duration. Certain parasitoids seem to oviposit successfully or find their hosts with ease only at specific times in the caterpillar developmental progression. If a parasitoid uses volatiles released at the time of moulting or cocoon spinning as host-location cues

(see Marsh 1937 for a probable case with cecropia moths), the length of time between moults may be irrelevant to the intensity of its threat. Mimics of urticators (e.g., *Santa Rosa saturniines* and most ceratocampines) and of vertebrate eyes (e.g., *Xylophanes* spp., *Eumorpha labruscae*, *Agrius cingulatus*, *Hemeroplanes triptolemus*) are intermediate cases. However, this is probably less true of the mimics of urticators since no amount of visual inspection can tell a monkey if a spiny mimic is in fact an urticator.

In summary, a new immigrant species of hemileucine saturniid might well have the opportunity to choose evolutionarily or ecologically a host list taking into account only the nutrient traits, conspicuousness, and microclimate of its potential hosts, while a newly arrived sphingid might not ever use many nutritionally suitable hosts because the carnivory regime on them is too severe given a low crypticity on the backgrounds they provide. Alternatively, the sphingid may stay tied firmly to a small subset of the hosts it can develop on because other hosts do not offer a growth rate quite as fast as those used (see below), given that particular sphingid's fine-tuned detoxification system.

Physiology of fast development time. *Santa Rosa* sphingid caterpillars are unexceptional in their development rates and variability in size at pupation. Even the largest only use four to five weeks for development, and the smallest (e.g., *Cautethia spuria*) as little as two weeks. Within a species there is little intra-sex variation in pupal weight (although by severe starvation bouts on low quality food in the laboratory, subnormal-size adults can be produced, and are found occasionally in nature as well). *Santa Rosa* saturniids differ from this pattern in three ways. They grow more slowly, the size of conspecifics at pupation is quite variable even on the best foods (except for hemileucines, which are more sphingid-like on this trait), and they appear to have an internal calendar that dictates the time of cessation of feeding (again, except in hemileucines). The non-hemileucines use 1.3–2.0 times as long to attain full-size as do sphingids of the same pupal weight. Hemileucine saturniids require as much as two to three times as long (up to 2.5 months) as do sphingids of the same body weight. For example, it takes 20 days of feeding to grow a 1.8 g female *Perigonia lusca* pupa on *Calycophyllum candidissimum* and 52 days of feeding to grow an *Automeris zugana* female pupa of the same weight on the same host plant side by side in the laboratory. A 20 g Puerto Rican *Pseudosphinx tetrio* caterpillar may be produced in as little as 24 days (J. A. Santiago-Blay, personal communication) while an *Eacles imperialis* caterpillar at *Santa Rosa* normally uses 30–40 days to attain this weight. As yet I do not know if such differences are due to the saturniids taking in less leaf material per 24 hours, getting less out of what they take in, or taking in overall lower quality materials (or all three). There is also the possibility that a living gram of saturniid pupa is more expensive than is a live gram of sphingid pupa because of different proportions of water, fats, etc., but I do not have the data to comment further on this point.

My working hypothesis is that saturniid caterpillars are often consuming phenol-rich foliage that yields relatively little assimilatable material per

bite because the leaf phenols have bound with the nutrients in the leaf and that the caterpillar has evolved food passage rates appropriate for such a low yield per bite kind of extraction. This stands in contrast to a sphingid caterpillar that can detoxify or otherwise avoid the primary defence chemicals of its food by, for example, enzymatically crunching up the toxin molecules or not assimilating them. It is then free to extract a much higher proportion of the nutrients in the meal (assuming that plants protected with toxic small molecules are low in foliar digestion inhibitors to bind with the nutrients). The caterpillar digestive physiology literature adds corroboration and complexity to such a view. Martin and Martin (1982, 1983) have quite appropriately emphasized that whether phenolic content of foliage is a reliable measure of how much of the leaf protein is unavailable to a caterpillar depends on the caterpillar gut pH as much as on the amount of phenolics and nutrients (and see Lawson *et al.* 1982). However, the fact remains that the Santa Rosa saturniids feed on some of the most phenol-rich plants in the Park whereas the sphingid hosts have very low phenolic levels and often contain alkaloids or other toxic small molecules (Janzen and Waterman 1984). In the saturniid hosts there is certainly the opportunity for nutrient binding (and indigenous gut chemical binding) by phenolics and apparently none for direct toxicity (except for *Copaxa* on *Ocotea*, see below), while the reverse is true for the sphingid hosts. Schroeder (1972) found growth efficiencies of the polyphagous cecropia caterpillar to be about half that of the sphingid *Manduca sexta*, and there is a growing body of examples that polyphagous caterpillars grow more slowly than do closely related monophagous caterpillars (e.g., Scriber 1979a, Scriber and Slansky 1981). While the causal relationship has yet to be discovered, it is also clear that caterpillars feeding on moister food have higher assimilation efficiencies and/or growth rates (Scriber 1977, 1978, 1979a, 1979b, 1979c, Scriber and Slansky 1981). The sphingid hosts at Santa Rosa have a significantly higher water content than do the saturniid hosts (Janzen and Waterman 1984).

The overlaps between the saturniid and sphingid host lists (between Table 3 and 4) are instructive. *Ocotea veraguensis* is perhaps the most confounding overlap, since it supports a monophagous saturniid and two monophagous sphingids. Furthermore, it is the only alkaloid-positive saturniid host discovered to date in the Park (a single record of *Automeris zugana* on *Solanum hazenii* is an exception, but *S. hazenii* is certainly not among the usual hosts of *Automeris zugana*). *O. veraguensis* has a very low leaf phenol content and I suspect that *C. moinieri* is behaving like a sphingid with respect to it (which is further evidenced by the apparent restriction of *Copaxa* to Lauraceae (Janzen 1984d), a sphingid-like generic oligophagy). *Calycophyllum candidissimum* is in the alkaloid-rich Rubiaceae and seemingly appropriately supports two sphingids. However, it is also a common host for *Automeris rubescens* and *Periphoba arcaei*; its leaves are not alkaloid positive and are the most phenol-rich of the Rubiaceae tested, though still quite low in phenolics (Janzen and Waterman 1984). That *Automeris zugana* can eat *Solanum hazenii* along with the great variety of other things on its host list suggests that sphingids are, however, not the

only large caterpillars that can detoxify or bypass alkaloids. The pest status of *Eacles imperialis* on Brazilian coffee leaves (Crocomo and Parra 1979) suggests the same.

If saturniids are tolerating a low rate of nutrient assimilation and thereby feeding on either many species of plants (hemileucines) or the leaves of large trees (low in water, high in phenolics, variable in nutrient content depending on where the leaf lies in the tree crown), there must be strong variation within and among species in the amount of nutrients that can be assimilated within the caterpillar stage. The Santa Rosa hemileucines express this by having highly variable growth rates and a consequence is that by the end of the rainy season their adult eclosions are poorly synchronized. The non-hemileucines express this by having a relatively fixed larval period and a variable pupal size with the consequence of relatively synchronous adult eclosions during the rainy season. In a group of *Rothschildia lebeau* siblings on the same individual host plant, for example, it is commonplace to obtain two-fold variation in male or female pupal weights yet have only three- to six-day variation in larval duration for most individuals. Size seems to depend on the luck of the particular leaves obtained. The caterpillars do not continue to grow until they reach some size near the average before pupating, and fortunate caterpillars do not bow out of larval life well before their thinner siblings. I suspect that the primary selection for such a pattern is the value of remaining in synchrony with the population, since the dis-synchronous saturniid cannot simply wait around until other adults eclose, or migrate to a different habitat. Spingids, with their longer adult lives and ability to obtain nutrients as adults, should place less value on synchrony and more on getting through the larval stage rapidly.

Saturniid avoidance of small life forms. In contrast with spingid caterpillars – which as a group are found on all sizes and ages of plants of all life form (Table 4) – Santa Rosa saturniid caterpillars are usually found in the crowns of adult and large host plants (non-hemileucines and some hemileucines) or host plants of all sizes with emphasis on large ones and adults (hemileucines) (Table 3). This ecological statement has two aspects. Is the saturniid caterpillar distribution generated by the eggs being laid in many places but the caterpillars only surviving in tree or treelet crowns? Or, are the adults programmed to oviposit primarily in adult plant crowns? Both cases occur at Santa Rosa. *Rothschildia lebeau* eggs can be found on *Spondias mombin* and *Exostemma mexicanum* from one to 20 m in height, but the caterpillars almost never survive carnivory on plants under about four m in height. On the other hand, there is no indication that *Syssphinx molina* and *S. colla* ever oviposit on sapling *Pithecellobium saman* trees; however, when the caterpillars are experimentally placed on saplings, they are almost invariably removed by carnivores before reaching pupation.

What is the difference between saplings and other small plants on the one hand, and adults and large plants on the other? At least for the 26 Santa Rosa saturniids reared to date, the foliage of saplings of their host

plants is quite adequate fodder, whether it is cut foliage in the laboratory or foliage on the tree inside a protective net.

To the ovipositing moth, saplings and little plants are much smaller targets than are adult crowns. A sapling is usually mixed in with many other plant species and produces a much smaller odour cue than does an adult tree. Once the target has been found, a sapling only has the resources for a few larvae; the female will have to locate many more of them (or her caterpillars will have to do the searching).

To the caterpillar the sapling or small plant offers limited choices for safe feeding and resting sites. Saplings often bear relatively sparse foliage and a large caterpillar is more conspicuous there than in dense clusters of leaves in a large tree crown. A sapling is also likely to be defoliated if several larvae are present. Defoliation not only threatens larvae with starvation but exposes the caterpillars to visually-orienting carnivores. Being intermingled with other species-rich and fast-growing vegetation, the sapling and small plant crown will be foraged through by carnivores more intensely than will be an equal volume of vegetation in the relatively sterile foliage of a large tree crown occupying as much as 0.5 ha. It seems appropriate that some of the strongly urticating and polyphagous hemileucines are the saturniids that have come to occupy the tangles of small plants so rich in carnivores at Santa Rosa. An exception is *Syssphinx mexicana*, a ceratocampine saturniid that feeds only in ant-acacias, shrubs and treelets of fast-growing secondary succession; however, *S. mexicana* may be unambiguously viewed as the most urticating saturniid of all, since the plants it lives on are heavily occupied by strongly stinging *Pseudomyrmex* ants.

But if life is so dangerous in low vegetation and on small plants, how do the sphingids survive there? First, many sphingids match their backgrounds extremely well and add dramatic larval colour polymorphisms to the mix as well (e.g. Schneider 1973). Second, some leave their hosts during the day to hide in the litter or on shaggy-barked stems (e.g., *Sphinx merops*, *Isognathus rimosus*, *Xylophanes anubus*, *X. ceratomioides*, *Aleuron carinata*). Third, by laying single eggs, the female sphingid gets more tries at finding locally carnivore-free micro-sites than does a saturniid laying the same number of eggs in large batches. Fourth, the sphingid caterpillar is exposed for a shorter time; a 0.7 g adult female *Perigonia lusca* may spend slightly less than three weeks on a *Calycophyllum candidissimum* sapling as a caterpillar while an urticating *Automeris zugana* weighing as much will be there six weeks (or longer). Fifth, if the right situation for oviposition does not present itself, the sphingid can delay oviposition or migrate out of the habitat. Finally, it may be that many of the cryptic sphingids are immune to repeated predation by vertebrates owing to having a gut full of toxic foliage. A small bird (e.g., *Campylorhynchus rufinuchus*, F. Joyce personal communication) may repeatedly search a *Calycophyllum* crown for *Perigonia lusca* caterpillars but pass up search opportunity for the very similar green caterpillars of *Callionima falcifera* on *Stemmadenia* simply because the later sphingid has

a gut full of alkaloid-rich foliage and would be a lethal lunch for a baby bird. *Isognathus rimosus* and *Callionima falcifera* also squirt very bitter fluids from glands on the body when molested (Haber 1983b, A. Pescador, personal communication).

In closing

This attempt to dichotomize saturniids and sphingids brings to mind several background questions of widespread application. Should we view the large-bodied moths termed Saturniidae as having evolved from a smaller non-feeding moth (as there are many of in the Bombycidae, Mimallonidae, Limacodidae, Lymantriidae, Lasiocampidae, Megalopygidae – moths that have many if not all of the traits attributed to saturniids in this essay) or from a large moth that feeds as an adult and has many other sphingid attributes? Does the dichotomy shed light on why most continental but local moth faunas contain roughly twice as many species of sphingids as saturniids, be they extra-tropical or tropical? Is it more reasonable to speak of a local fauna of saturniids than sphingids (or neither)? In general I think we do not yet know enough of the natural history of these moths to construct elaborate or definitive answers to questions such as these. However, a small try may be of value in encouraging the gathering of relevant data by those around the world with the moths in their hands.

The evolution of a large saturniid from a small saturniid-like moth is neither difficult to imagine nor particularly helpful in understanding the evolution of the non-feeding adult habit in the first place. However, the evolution of non-feeding has two possible interesting routes. On the one hand it may have occurred in a habitat exceptionally favourable to larval survival, creating a situation that favoured mutants that remained longer as larvae and enclosed as more egg- and fat-laden adults. Such adults would be able to give rise to the next larval stage faster and perhaps even be less competent as resource gatherers and exacting ovipositors. On the other hand it may have occurred in a habitat exceptionally unfavourable to adult survival. Selection would be intense for larval traits that allowed a long stay in this resource-gathering stage. The ideal habitat for the evolution of a saturniid-like organism out of a sphingoid lineage would then be one with both exceptionally good conditions for larval survival and exceptionally harsh conditions for adults. In the progression from deserts to tropical rainforests, arid lowland forest would seem the most ideal for such an evolutionary event (with, for example, a quick-flushing deciduous legume tree as the host), though not the habitat in which the most species could co-occur once the life form is evolutionarily established.

Such reasoning is also pertinent to the question of why there are about twice as many sphingid as saturniid species in most lowland continental habitats. One way to create favourable conditions for a large adult moth is to give the adult the ability to search widely for local good conditions, and sphingids have this ability. In a certain sense, Santa Rosa does not have a

breeding population of 61 species of sphingids, since many of those that breed in Santa Rosa seem to leave for at least part of the year. Understanding their species richness in Santa Rosa requires knowledge of all of Costa Rica, and were Santa Rosa an isolated island, its breeding species richness of sphingids would be severely reduced. Saturniids, in contrast, maintain a breeding population at Santa Rosa without migration, though it is quite possible that the strong-flying males move genes about over an area considerably greater than that of the Park and that local extinction occasionally occurs but the population is re-established by local movements of females. It is then more reasonable to speak of a local fauna of saturniids than of sphingids.

Such an inquiry brings to mind the age-old question of whether a widespread species is made up of many local populations specialized to local conditions or of a sufficiently plastic phenotype and all-purpose genotype that its members' responses to locally different ecological circumstances are sufficient for survival (Fox and Morrow 1981). In the case at hand, saturniids appear to have the lack of vagility which predisposes them for the former, while sphingids appear to be the opposite. However, a closer look at saturniid biology suggests the reverse. Many, with hemileucines at the top of the list, should be able to drop into just about any habitat and find some plant, among a variety of families, on which the larvae can feed. In contrast with sphingids, adult hosts are not needed. Barriers to geographic range extension should be based on climate and the balance of carnivory against the output from the particular edible hosts. Likewise, sphingids may be doing the opposite trick of laboriously seeking out the relatives of some suite of closely related plants in each new habitat invaded; given that such a relative and adult nectar resources can be found, the moth can persist. While it certainly has to deal with the climate and carnivory regimes, it has the option of vacating the habitat for part of the year, and both its caterpillars and adults may be able to survive under an overall greater intensity of carnivory than can the saturniids. Such a scenario is consistent with the observation that many sphingids have taxonomically narrow host lists (though perhaps containing many species) over tens of degrees of Latitude (e.g., the larval host records of Moss (1912, 1920) in Peru and Brazil, and mine in Santa Rosa are almost identical at the genus and family level). In contrast, the aggregate host list of a widespread saturniid may contain tens of families of plants or be as narrow as one of a sphingid.

If ever-sharpening focus on the Santa Rosa saturniid and sphingid faunal portrait bears out the general pattern that I think I perceive at this beginning, are there reasons to believe that a similar close look at these moths in some other tropical area will reveal a different portrait? Certainly even a pristine tropical island fauna cannot show the Santa Rosa contrast since the saturniids are largely missing from islands. The upper part of a tropical continental mountain range will likewise be of no use as it will lack sphingids (except for migrants passing through) at the 2500 m-plus elevations that still have one to five breeding saturniids. As already emphasized, a lowland rainforest site will lack the strong seasonal element

that gives the Santa Rosa portrait part of its distinctive complexity. While the species richness ratios of saturniids to sphingids tend to be about 1:2 for most lowland neotropical sites for which there are data, taken as a whole, large tropical land masses have equal numbers of each family or even more saturniids (e.g., Mexico appears to have about 148 species of saturniids and 154 species of sphingids (Hoffmann 1942); C. Lemaire (personal communication) estimates 850 saturniids and 500 sphingids for the New World).

A quick glance at other continents suggests important similarities and differences. Three African saturniids have beaten the mating game by becoming parthenogenic (Lemaire 1969, Pinkey 1972). The life forms of old world adult tropical sphingids and saturniids contain many close copies of those of the Neotropics; old world tropical saturniid caterpillars are often urticating (or apparent mimics) and the sphingid caterpillars bear the same close similarity to their substrates as do the Neotropical ones. However, there is at least one conspicuous cautionary difference. Not only do the 61 species of breeding Santa Rosa sphingids not use legumes as larval hosts (despite the fact that the Santa Rosa flora is 20 per cent legumes (Janzen and Liesner 1980)), but legumes are conspicuously missing from all New World sphingid larval host lists. In contrast, of 135 sphingids whose larval hosts were recorded in India, Sri Lanka and Burma (Bell and Scott 1937), 10.4 per cent fed on legume foliage. Likewise there are several legume-eating sphingids in Ivory Coast foliage (Vuattoux 1978). A second example of discordance is that the saturniid:sphingid species ratio in this rainforest is 27:62 (Vuattoux 1978, 1981) and therefore consistent with this ratio in lowland Costa Rican rainforest sites (Haber 1983a, sphingids; Janzen collection records, saturniids). However, it also appears that 42 per cent of the Ivory Coast rainforest sphingids do not come to light (Vuattoux 1978), as compared with four per cent at Santa Rosa. While neotropical islands characteristically lack saturniids, those of the Asian tropics have a small but conspicuous saturniid fauna (Peigler 1983).

The saturniid-sphingid comparison should differ in various ways outside the tropics. Extra-tropically there are more diurnal special in both families, less species-rich and life-form-rich vegetation types from which the moths may choose their larval hosts, more kinds of and longer severely inimical seasons, and more pulsed carnivore regimes. In areas sufficiently extra-tropical that there can be only one generation per growing season, with the inimical season serving as an omnipresent synchronization event, the saturniid larva and pupa are not under selection for the use of an internal calendar and I expect the consequence to be larval and pupal stages that are more intra-specifically variable in duration (e.g., Worth *et al.* 1979).

At the end, I can only lament that it is already too late to explore the kinds of questions I have raised in this essay. An attempt to understand extra-tropical saturniid and sphingid faunas in the eco-evolutionary context presented here will be almost entirely an act of reconstruction, a reading of post-Columbian anachronisms. How does one move from Waldbauer and Sternburg's elegant and detailed examination of cecropia moth urban

ecology to understanding how that moth evolved and in concert with what other saturniids and sphingids. Illinois is only a zoo with no feeding and heating bill. As long as tropical patches of relatively pristine habitat still remain, it is tempting to think that there is some chance. However, the reality is that they will be gone within a few decades and the small dots that will be saved by intensive efforts will have quite different ecologies from those that they had for millennia before. Imagine how many migrant moths would have been attracted to that light that I placed in the 1800 m Costa Rican pass on 4 December 1983, were I to have put it there when 90 per cent of the source area was not pasture and crop fields as it is today. Yes, Santa Rosa will remain as a National Park, but from where are the migrant sphingids going to come at the beginning of each rainy season when their source area is lush agricultural land providing a high standard of living for this relatively well-to-do tropical country?

Acknowledgements

This study was supported by NSF grants DEB 77-04889, DEB 80-11558, and BSR 83-08388, and by the Servicio de Parques Nacionales de Costa Rica. The following people were especially helpful in discussing the ideas and commented constructively on the manuscript: W. A. Haber, C. Lemaire, G. P. Waldbauer, J. G. Sternburg, R. S. Peigler, G. Stevens, W. Hallwachs, and M. O. Johnston. R. S. Peigler aided greatly in locating pertinent references. I was substantially aided in field work by W. A. Haber, M. O. Johnston, W. Hallwachs, R. Espinosa, G. Vega, T. Gush, R. Glass, M. L. Higgins, T. Fleming, F. Joyce, J. Howard, E. Arce, P. J. DeVries, Santa Rosa park guards, and others who have brought me caterpillars. I dedicate this essay to all those future tropical generations who will never see many of the things discussed here unless some severe and dramatic changes occur in tropical social attitudes on how much of the remaining forest should be converted to money, children and hamburgers.

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Fig. 1. Representative Saturniidae breeding in Santa Rosa National Park, Guanacaste Province, Costa Rica. All specimens were wild-caught. Rule is 4 cm long. 1. *Copaxa moinieri*, female. 2. *C. moinieri*, male. 3. *C. moinieri*, male. 4. *Othorene purpurascens*, female. 5. *O. purpurascens*, male. 6. *O. purpurascens*, male. 7. *Eacles imperialis*, female. 8. *E. imperialis*, male. 9. *Rothschildia lebeau*, female. 10. *R. lebeau*, male. 11. *R. lebeau*, male. 12. *Dirphia avia*, male.

Fig. 2. Representative Saturniidae breeding in Santa Rosa National Park, Guanacaste Province, Costa Rica. All specimens were wild-caught. Rule is 4 cm long. 1. *Adeloneivaia isara*, female. 2. *A. isara*, female. 3. *A. isara*, female. 4. *A. isara*, male. 5. *A. isara*, male. 6. *A. isara*, male. 7. *Hylesia lineata*, female. 8. *H. lineata*, male. 9. *H. lineata*, male. 10. *H. lineata*, male. 11. *Copiopteryx semiramis*, male. 12. *Syssphinx mexicana*, female. 13. *S. mexicana*, male. 14. *S. mexicana*, male. 14. *Schausiella santarosensis*, male. 16. *Ptilocola dargei*, female. 17. *P. dargei*, male. 18. *Titaea tamerlan*, female. 19. *T. tamerlan*, male. 20. *Automeris rubrescens*, female. 21. *A. rubrescens*, male.

Fig. 3. Representative Sphingidae breeding in Santa Rosa National Park, Guanacaste Province, Costa Rica. All specimens were wild-caught. Rule is 4 cm long. 1. *Manduca lefeburei*, female. 2. *M. lefeburei*, male. 3. *Xylophanes pluto*, female. 4. *X. pluto*, male. 5. *Aellopos titan*, female. 6. *A. titan*, male. 7. *Erinnyis obscura*, female. 8. *E. obscura*, male. 9. *Amplipterus ypsilon*, female. 10. *A. ypsilon*, male. 11. *Manduca corallina*, female. 12. *M. corallina*, male. 13. *Xylophanes ceratomioides*, female. 14. *X. ceratomioides*, male. 15. *Eupyrhroglossum sagra*, female. 16. *E. sagra*, male. 17. *Enyo ocypete*, female. 18. *E. ocypete*, male. 19. *Callionima falcifera*, female. 20. *C. falcifera*, male. 21. *Manduca sexta*, male.

Fig. 4. Representative Sphingidae breeding in Santa Rosa National Park, Guanacaste Province, Costa Rica. All specimens were wild-caught. Rule is 4 cm long. 1. *Aleuron iphis*, male. 2. *Xylophanes tersa*, female. 3. *X. tersa*, male. 4. *Agrius cingulatus*, female. 5. *A. cingulatus*, male. 6. *Cautethia yucatanana*, male. 7. *Cautethia spuria*, female. 8. *C. spuria*, male. 9. *Nyceryx coffeae*, female. 10. *N. coffeae*, male. 11. *Perigonia lusca*, female. 12. *P. lusca*, male. 13. *Protambulyx strigilis*, female. 14. *P. strigilis*, male. 15. *Pachylia ficus*, female. 16. *P. ficus*, male. 17. *Cocytius lucifer*, female. 18. *C. lucifer*, male. 19. *Celerio lineata*, female. 20. *Xylophanes porcus*, female. 21. *X. porcus*, male. 22. *Aleuron chloroptera*, male.



Fig. 1



Fig. 2



Fig. 3

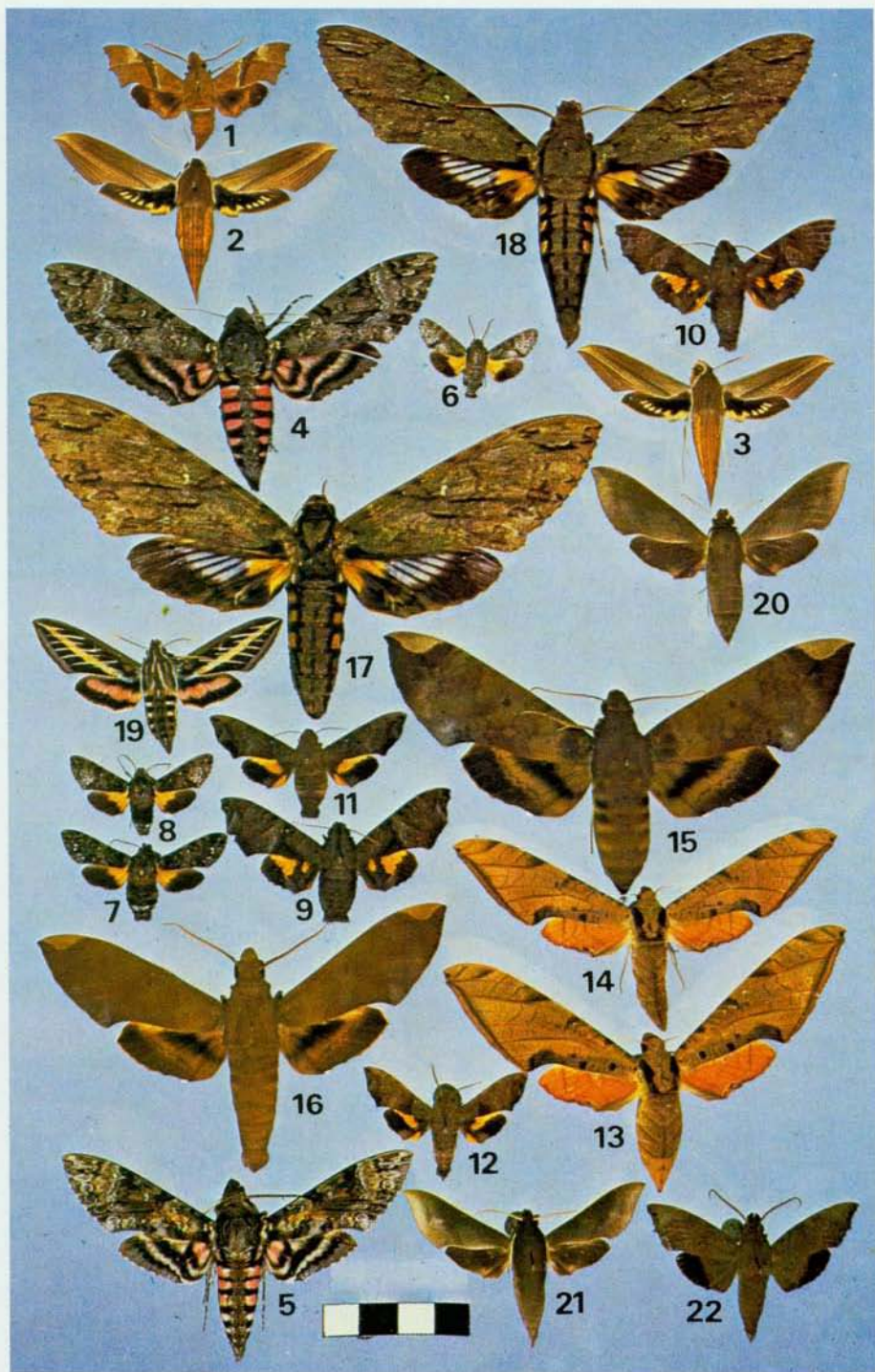


Fig. 4