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BIOGEOGRAPHY OF AN UNEXCEPTIONAL PLACE: WHAT DETERMINES THE SATURNIID AND SPHINGID MOTH FAUNA OF SANTA ROSA NATIONAL PARK, COSTA RICA, AND WHAT DOES IT MEAN TO CONSERVATION BIOLOGY?

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ABSTRACT

Santa Rosa National Park is an arbitrarily defined 108 km^2 patch of dry forest in the northwestern Pacific coastal lowlands of Costa Rica. It has a saturniid moth fauna of 30 breeding species (and 5 waif species) and a sphingid moth fauna of 64 regularly breeding species, 10 occasional breeding species, and 9 waifs (83 species in total). There is one endemic saturniid and no endemic sphingids. Furthermore, nearly all of the saturniids and sphingids of Santa Rosa have very broad geographic and ecological ranges. The saturniids are dormant during the six month dry season and all survive the dry season within the Park. More than half of the sphingids migrate out of the Park during the dry season or even the second half of the rainy season. This migration is an integral part of Santa Rosa's interdependency with the rainforest parts of Costa Rica (and vice versa).

What determines the ceiling to the number of species of saturniids and sphingids in Santa Rosa? The Park is not isolated. There are no inhospitable barriers to potential colonizing species in the immediately adjacent rainforest (10-15 km to the east). This rainforest is occupied by at least 25 species of saturniids and 52 species of sphingids that also breed in Santa Rosa. Why don't the other rainforest saturniids and sphingids move into Santa Rosa, at least during the rainy season? There is no suggestion that direct competitive interactions prevent the 31st or 65th species of saturniid or sphingid from moving into Santa Rosa. Likewise, there appears to be a sufficient array of food plant species for the potential invader to find food. However, Santa Rosa supports a formidable array of predators and parasitoids that eat saturniid and sphingid caterpillars. On the one hand, this array is sufficiently depressed by the dry season that the breeding saturniids and sphingids can produce 1-2 generations. It is probably to make use of the relatively carnivore-free early wet season that so many sphingids migrate into the park at the start of the rains. On the other hand, the carnivore array contains enough specialist and semi-specialist parasitoids to provide the density-dependent mortality that could be regulating the overall species richness of saturniids and sphingids. There are numerous species of parasitoids whose density or foraging intensity could increase were a 31st saturniid or 65th sphingid to be added to the Santa Rosa breeding array of moths. This increase could prevent the moth's entry or eliminate a resident.

Santa Rosa is to be viewed as being in a biologically interdependent state with other habitats in Costa Rica, to say nothing of the adjacent dry forest. If for example, Costa Rican rainforests are no longer present to generate and absorb migrants from Santa Rosa, there will be second and third order impacts on the year-round resident fauna and the ecological structure of the Park.

Introduction

My goal is to understand the forces that produced and maintain the arrays of organisms found in the habitats in Santa Rosa National Park. This Park is a 10,800 ha block of hilly lowlands (0-350m elevation) on the Pacific coastal plain of northwestern Guanacaste Province, Costa Rica (Fig. 1) (Boza and Mendoza 1981, Hartshorn 1983, Janzen 1982, 1983, 1984a-c, 1985a-b, Heithaus and Fleming 1978, Gómez 1986). Santa Rosa is not a mountain top, take, single habitat or any other kind of island that is ecologically discrete. Until very recently, it was a simply an arbitrarily delimited small portion of a large and continously forested landscape that is patchily heterogeneous with respect to soil type, drainage, slope, precipitation, wind exposure, elevation, evergreenness, proximity to rainforest, etc. Within 20 years or less it will be an abruptly and thoroughly distinctive ecological island, surrounded by an ocean of pasture and farmland.

Here I examine what is presently known of the ecologies and geographic ranges of the saturniid and sphingid moth faunas of Santa Rosa. I intend to draw attention to perhaps more plebian questions that have of recent been pushed to the side by more spectacular concerns of island biogeography, vicariance theory, disjunct distributions, etc. (e.g., compare Udvardy 1969 with MacArthur and Wilson 1967, Savage 1982, Brown and Gibson 1983). As an ecologist, I find that one of the largest puzzles in biogeography lies in the question of why so many tropical animals do not expand their ranges into seemingly suitable habitats. Finally, I examine some unpleasant implications of the answer to this question for conservation biology in tropical habitats.

The Santa Rosa moth fauna

Portions of Santa Rosa have been variously logged, farmed and pastured since at least 1726. In 1978, the last major cattle population was shot out of the Park and the various ages and kinds of vegetation began the long process of woody succession to a forest cover that will eventually range from 2 to 30 m in height in an intact state. The source of colonists for this succession range from tiny patches of nearly intact forest to large areas of secondary succession rich in fast-growing and ruderal species of plants, and in remmants of populations of species that are more characteristic of intact forest. The original habitat types of Santa Rosa (and most of Santa Rosa's successional habitats) were characteristic of a lowland dry to semi-deciduous forest belt extending at least from the tropical lowlands of Mexico down the Pacific coast of Mesoamerica to central Costa Rica, with outliers on the Caribbean sides of Guatemala, Belize, Honduras, and Venezuela, and on the Pacific sides of Panama and Colombia.

The habitats of Santa Rosa range from very deciduous (Fig. 2) to nearly evergreen during the 5-6 month rain-free dry season and have a moth fauna of about 2760 species (Janzen 1985b; plus about 380 butterflies, DeVries 1983 and the present study). Recall that the area of the Park is about 108 km^2. This fauna may shrink a bit as the various ages of diverse kinds of woody secondary succession in pastures and fields return to pristine forest (a process requiring thousands of years). It may be viewed as a normal lowland Pacific coastal (dry forest) moth fauna for the area from tropical lowland Mexico to at least Panama City. While all the votes are not yet in, our ongoing survey (D.H. Janzen and W. Hallwachs) of the moth fauna of Costa Rica suggests that Santa Rosa has 80-100 percent as large a moth fauna as does any other lowland Costa Rican area (wet or dry forest) of comparable size and disturbance history.

This moth fauna contains 30 species of breeding saturniids and as of August 1984, 5 species of waif saturniids (Table 1). Likewise, it contains 64 species of breeding sphingids that are present each rainy season and 19 species whose adults and larvae are occasional breeders, waifs or transients (Table 2). The saturniids and sphingids are the portions of the moth fauna taht I know best (e.g., Janzen 1981a, 1982, 1984a-c, 1985b, Janzen and Waterman 1984) and are best known taxonomically and geographically (e.g., Lemaire 1971-1976, 1978, 1980, 1987, Schreiber 1978). The Santa Rosa fauna contains as many or more saturniids and sphingids as can be found in either the east or west half of North America north of Mexico (Hodges 1971, Ferguson 1971, 1972). However, all indications are that with more facts at hand, this essay and its conclusions could also have been based on other families of moths that are species-rich at Santa Rosa, such as Notodontidae, Noctuidae and Pyralidae.

As will become clear, the biogeographical ecologies of the saturniids and sphingids of Santa Rosa are quite different, so I will discuss them separately.

The Santa Rosa saturniids

Where do they come from?

Santa Rosa does not have a local, endemic fauna of saturniids (Table 1). Furhermore, this absence of small-scale endemism is characteristic of the 18 other low to mid-elevation Costa Rican sites that we have surveyed. Only one of the 30 breeding species at Santa Rosa, *Schausiella santarosensis* (Ceratocampinae) (Lemaire 1982), is endemic to the immediate vicinity. The other 29 species have breeding distributions covering tens of degrees of latitude. Three species - *Automeris io, Eacles imperialis, Rothschildia lebeau (R. forbesi* of some older literature, Ferguson 1971, 1972) - range into the United States as breeding and permanent overwintering populations. *E. imperialis* breeds from Canadá to Argentina (Lemaire 1985).

Something about 100,000 years ago, Santa Rosa was catastrophically covered with a 50-100 m thick layer of volcanic ash, tuff, mud and lava blown out of the volcanic complex to the east (Volcán Orosi, Volcán Cacao, Volcán Ricón de la Vieja) (Janzen 1985a). At that time, the climate of Santa Rosa was presumably about the same as that of hilly lowland tropical Mexico and the Pacific coastal plain of Central America, just as it is now. Within the Park, one encounters much of the variation in climate and vegetation that is encountered over this large latitudinal range. For example, the intact forest ranges from 2-4 m tall and otally deciduous thorn scrub (on the dry serpentine and volcanic ridges near the coast) to 20-30 m tall semi-evergreen closed canopy forest (Janzen 1985a). The dry season is about six months long and intense (Fig. 2-3), and the rainy season usually has a dry season of several weeks duration in its middle (the veranillo). The total annual rainfall at Santa Rosa varies from 900-2300 mm of rain (unpublished weather station records).

This catastrophically bared site was then invaded by the available fauna and flora. Whatever longterm changes in climate, associated with glaciation cycles or otherwise, have occurred at Santa Rosa since this colonization, they did not generate any kind of local fauna (or flora). The contemporary resident saturniids are the endemic *Schausiella santarosensis,* four dry-land species characteristic of the Central American coastal plain *(Syssphinx mexicana, Citheronia lobesis, Adeloneivaia isara, Automeris zurobara)*, and 25 ecologically widespread (cosmopolitan) species that are breeding residents from Costa Rica's driest sites to its very wettest lowland rainforests (and over a comparably broad ecological range elsewhere in the Neotropics). Allocation of *S.mexicana* to the category of 'dry-land species', rather than 'cosmpolitan', has to be seen in the context of the fact that its range only occasionally extends into more moist forest on those occasions where its ant-acacia host plants do (e.g., in some parts of Chiapas, Mexico). By definition, stricly rainforest species of saturniids cannot occur at Santa Rosa, since by maintaining year-round populations in dry forest as well as in rainforest they are by definition cosmopolitan. The widespread nature of these moths is also illustrated by the early date on which they were firest described by taxonomists (Table 1); they were quickly encountered by the firest neotropical collectors because of their widespread distributions as well as because of their large size.

The four non-endemic dry forest species of saturniids, then, are at Santa Rosa simply because Santa Rosa is (was) part of a continous belt of dry forest. They invaded along with the vegetation after volcanic devastation, show no sign of being very recent arrivals and are always present. No evolutionary change was needed or likely for them to invade Santa Rosa. If they exist elsewhere broadly sympatric (not parapatric) with other dry forest saturniid species that are missing from Santa Rosa, it is at some site that is many hundreds of kilometers away (and isolated by blocks of evergreen rainforest on the Panama-Costa Rica border, and between the Panamá Canal and the Panama-Colombia border). Because these other dry forest species are in some distant and substantially drier site, they are not probing Santa Rosa with saturniid propagules. There simply is no opportunity for them to attempt and then fail to establish because a) they cannot evolve a distinctive Santa Rosa population owing to a massive genetic connection with the parent population or b) the ecological conditions are just not right.

The 25 ecologically cosmopolitan species (Table 1) could have, and probably did, reinvade Santa Rosa from both the wetter and drier portions of their ranges (i.e., from all directions but the ocean). The adults of the Santa Rosa portions of a saturniid species are commonly somewhat different in aspect from those of the wetter parts of Costa Rica, but these differences could be either simple ecological responses by a general-purpose genotype to the dryness of Santa Rosa, or actual genetic differences in the Santa Rosa population, or both. For example, at least three species of Santa Rosa cosmopolitan saturniids are seasonally polymorphic; they have light-colored adults when the weather is dry, while during wet weather the morphs are almost as dark as are their rainforest conspecifics (e.g., Janzen 1984a). Also, Santa Rosa adults of almost all of these 25 cosmopolitan species are commonly smaller and lighter in color than are their wet forest conspecifics, irrespective of the weather or season.

Such differences in seasonal and regional plymorphisms could be purely phenotypic yet be based on a general-purpose genotype that is functional over a very wide ecological and geographic range; such a genotype may have evolved in a highly seasonal dry forest habitat at the time when each of these species was still a small isolate somewhere, and then been retained as the species spread geographically and ecologically. Alternatively, such traits could be specific genetic traits possessed only by the dryland portions of these ecologically cosmopolitan species. Only reciprocal transplant experiments can determine to which category the traits of each species belong.

However, there is a third source of Santa Rosa species, a source that is very relevant to the question of what determines how many species of saturniids are in Santa Rosa. The strictly rainforest saturniids in the rainforests 10-15 km to the east of the Park are continually arriving at the edges of the dry forest in which Santa Rosa is imbedded. At any time, one of these could develop a mutant that can use the Santa Rosa-type habitat and therefore extend that species range into a dry site. By definition, this would convert the species from a rainforest to a cosmpolitan species. Such an invader would then likely spread up and down the Pacific coast as well. I will discuss this route in more detail below. Alternatively, such an invasion could occur elsewhere along the coast and then the species could spread to Santa Rosa via the coastal dry forest margin. However, the possibility of the production of another Santa Rosa resident in this manner is now largely theoretical since virtually all of the relevant dry forest of Central America has been destroyed. Even Santa Rosa, still marginally abutting on ever more rainforest-like vegetation to the east and northeast, is rapidly receding from the rainforest mainland.

In summary, the Santa Rosa saturniid fauna, except for *S. santarosensis,* is 87 percent cosmopolitan with only a small contribution by purely dry forest species.

Schausiella santarosensis

This moth was firest collected in 1978, when the first thorough moth collections were made in the Park. Described in 1982 (Lemaire 1982), it is an unambiguous and unexceptional member of the genus *Schausiella.* However, *Schausiella* is quite a peculiar genus among saturniids; it ranges from Costa Rica to Bolivia and southeastern Brazil and is speciose (11 species), yet each species is usually rare (at least in collections) and many occupy small geographic areas as compared with ceratocampine saturniids in general (Lemaire 1987).

There are only two species of *Schausiella* known to breed in Costa Rica. One, *Schausiella denhezorum,* is represented in Costa Rica by a half dozen specimens from mid-elevation very wet rainforests on the Caribbean slopes (in Braulio Carrillo National Park at 700-1100 m elevation, La Montura and Estación Carrillo, F.G. Stiles and I. Chacón, collectors; Juan Viñas, Cartago Province, W. Schaus collector). The other, *S. santarosensis,* would likewise be known from only a few specimens except that I now know its life history and can therefore collect it in large numbers at specific places in Santa Rosa or immediately to the east during a few weeks of the year.

Biogeographically, what does *S. santarosensis* offer of interest? First, it is a spectacular demonstration that a highly host-specific monophagous insect may occupy only a tiny fraction of the geographic distribution of its host plant (cf. Strong *et al.* 1984 for several British examples of this phenomenon, and Johnson and Janzen (1982) for a Central American example). *S. santarosensis* caterpillars eat only the leaves in the crowns of adult *Hymenaea courbaril* trees (Caesalpinoideae: Leguminosae). Since the only other known host record for the genus, *Schausiella arpi,* is a laboratory rearing on the leaves of *Hymenaea courbaril* in southern Brazil (Lemaire 1985; H.R. Perason, personal communication), it is tempting to postulate that *Schausiella* is a caesalpinoid legume specialist (at Braulio Carrillo, there are no *Hymenaea* for *S. denhezorum* to feed on but there are other caesalpinoid legumes).

H. courbaril ranges as a common tree from the lowlands of tropical Mexico through Central America to southern Brazil (e.g., Lee and Langenheim 1975, Pennington and Sarukhan 1968). Why is *S. santarosensis* stuck on one little dot of this distribution in northwestern Costa Rica? The mystery is even more puzzling in that in the vicinity of Santa Rosa, *H. courbaril* ranges from evergreen and quite wet forest at 350-500 m elevation on the western slopes of Volcán Cacao (10-15 km to the east of the Park) to remnants of nearly deciduous primary forest on very dry southeast-facing slopes at 200 m elevation in the Park. *S. santarosensis* occurs throughout this broad ecological range (but tiny geographic range), an ecological range that appears to represent much of the ecological range of *H. courbaril* from at least Mexico to Panama (and much of South America).

What does this little dot of *S. santarosensis* suggest about the evolution of saturniid species? First, *S. santarosensis* could be a remnant of a once-widespread *Schausiella* species, a remnant that is now evolving some sort of close fit to its local situation. But if this is so, whatever could have eliminated our hypothetical and ecologically generalist parental species over most of its geographic range? Second, *S. santarosensis* could have been derived from a species that occasionally has eruptive migrations of females, the kinds of migrations that would occasionally place a colonizing population in a habitat that is suitable but generally surrounded by an ocean of unsuitable habitat.

Two facts bear on the above hypothesis. First, in 1978 (a year of exceptionally high moth density at Santa Rosa) numerous *S. santarosensis* appeared as fully gravid females at house lights at a distance of 300 m to the nearest adult *Hymenaea courbaril* and 600 m to the nearest approximation to a *H. courbaril* population of adult trees. While I presume that these females came from within the Park they could have been making an even longer flight if they came from the portion of the *S. santarosensis* population to the northeast of the Park. For fully gravid saturniid females, and especially for *S. santarosensis* females, such flight distances are exceptionally long. Some kind of eruptive 'migration' might have been occurring (no males appeared at the same house lights). C. Lemaire (personal communication) also noted exceptional numbers of two other species of female (*Schausiella* arriving at lights on rare occasions in Panama and Venezuela. Second, *S. santarosensis* is an ordinary saturniid in its detailed biology except that it displays the amazing behavior of having only one generation at the beginning of the rainy season (during the first two months) and then virtually all of the population remains dormant as pupae for the remaining four months of the rainy season and the following six months of the dry season; during this time its host plants stand in full green leaf for 11.5 months. These leaves are highly edible to *S. santarosensis* caterpillars obtained from eggs from females that are out of synchrony with the rest of the population. This species of moth is either very finely adjusted to unapparent details of the weather/carnivore/host interaction at Santa Rosa or is running on a program adjusted to other (past?) environments and has not changed to make use of the resources currently available.

Whatever its history, *S. santarosensis* appears to be a species that could continue to evolve in response to local selective pressures until it serendipitously becomes a genotype that is robust with respect to, for example, the broadly distributed environment of *H. courbaril;* at that point it could easily transform from a local endemic to a widespread dry forest species, and do it overnight on a geological or ecological time scale. Such an event would be reasonably viewed as a punctuation of an equilibrium, except that there is no reason to believe that *S. santarosensis* is in evolutionary equilibrium with the local habitat to which it is endemic. Rather, it would be a punctuation of a geographic equilibrium. Alternatively, a *S. santarosensis* genotype might appear that would allow it to spread rapidly over the (probably large) range of the unknown rainforest host tree of *Schausiella denhezorum* in Costa Rica's Braulio Carrillo National Park, thereby again transforming overnight a local endemic into a widespread cosmopolitan species, or at the least into a rainforest species with a dry forest outlier.

In summary, then, 1/30th of the Santa Rosa saturniid fauna could be a remnant of a once cosmpolitan or dryland widespread species, or it could be a species that has very peculiar local requirements (unrelated to simple host plant presence) but eruptively migrates at times and thereby occasionally places colonizers in isolated suitable habitats where yet again speciation may occur. Whatever its history, if Santa Rosa National Park had been placed 50 km to the north or south, *S. santarosensis* would have disappeared without a trace as the forests it occupies were (are) converted to pasture). In this case, Santa Rosa would be as free of endemic saturniids as it is of endemic sphingids. We will never know what other species of local saturniids analogous to *S. santarosensis* were extinguished during the elimination of nearly all of Mesoamerica's dry forest in the past 400 years.

What are the waifs?

To understand the waif or stray saturniids and their significance at Santa Rosa, a few points about saturniid adult biology need elaboration. Adults of both sexes do not feed and they live only 5-10 days. The virgin females 'call' males with pheromones at the site of eclosion on the night of eclosion (and on subsequent nights if not mated) and the males course widely across the habitat (or habitats) in search of females. Females rarely fly until after mating, and all circumstantial evidence suggests that they fly only very short distances (less than 1 km) when searching for oviposition sites (see Janzen 1984b for elaboration on these saturniid traits). This kind of reproductive biology has several biogeographic consequences.

1) If one is capturing saturniids at lights (or with traps baited with vigin females), males can be captured regularily in inhospitable habitats lying between the habitats that contain larval food plants and females. On a larger scale, wide-ranging (searching) males can be blown or perhaps even fly directly into inhospitable habitats many kilometers from their breeding habitat. That this is not fanciful is suggested by the fact that marked male *Rothschildia lebeau* have been captured as

far as 13 km from their release points within the Park (study in progress), and it is only 10-15 km east (and upwind) from the Park boundary to evergreen forest on the lower slopes of the volcanos.

There is no doubt that rainforest male saturniids occasionally wander into Santa Rosa's dry forests. Two males of *Rothschildia orizaba,* a strictly rainforest species in Costa Rica, have been taken during four years of moth census at two lights in the Park; both males had the kind of wing wear that is characteristic of the windy mid-elevation evergreen forests of the volcanos to the east. The other rainforest waifs, one *Hylesia hamata,* one *Hylesia umbrata,* one *Automeris hamata* and six *Adeloneivaia jason,* have all been males. In short, waif saturniids are males.

In strong contrast to the sphingids to be discussed below, there is no hint of regular migration by either sex of any Santa Rosa saturniid species. The relevance of all of this to biogeography is that capture data of saturniids, almost always based on males, must be treated with extreme caution in defining the ecological or geographic range of a species. Species that are represented by only a few male individuals at long intervals are likely not to represent a breeding population, provided they have a representative tropical saturniid natural history (e.g., diurnal or semi-diurnal lowland tropical species such as *Automeris phrynon* (Marquis 1985) or *Rothschildia erycina* do not conform to this rule). On the other hand, females are a very good indication of a breeding population; at eclosion, they are heavily laden with eggs, they lay most of their eggs in the first 1-3 nights after mating, they remain in the habitat where the larvae feed, and they appear to remain within a few hundred meters of their site of eclosion.

2) Male saturniids cannot colonize a habitat that lacks conspecific females. Furthermore, a waif is 'dead' the moment it permanently leaves the area of virgin females; its behavior as a waif cannot therefore be selected for. It is like a rainforest tree seed that washes into a river and out to sea; yes, it is being dispersed but it was 'dead' the minute it hit the water and whatever traits led to this dispersal are not being selected for by the "dispersal".

3) Waif saturniids are, however, a manifestation of widespread searching for mates by male saturniids. This widespread searching suggests an amelioration of the potential genetic effects of the intensely sedentary nature of the female portion of the saturniid population. It is reasonable to suspect that each occupied habitat has its own resident set of female lineages, a set that is sufficiently isolated through its members' lack of movements to become locally adapted. However, the males moving broadly among occupied habitat replicates will greatly reduce the chances for the local genetic differentiation of female lineages that could occur were only the females to be considered.

The very short life span of a saturniid is in itself a barrier to gene flow, since no matter what the average nightly movement, the moth will move a lesser distance than will a species of equal mobility but with a long adult life span (such as a sphingid, see below). The same habitat is more of an island to a saturniid than it is to a sphingid, for this reason alone.

If not by waifs, then how do saturniids invade?

At the eastern edge of Santa Rosa, where the Park borders on the ever more evergreen forest on the volcano foothills, there is a belt of dry but semi-evergreen forest 10-15 km in width that must be frequently invaded by females of stricly rainforest saturniids (e.g., *Eacles ormondei, Automeris celata, A. belti, A. banus, A. postalbida, A. phrynon, Adeloneivaia boisduvalii, Arsenura batesii, Copaxa rufinans,* etc.), moving only a few hundred meters to the west of their contemporary permanent breeding habitats. The boundaries of the distributions of the rainforest saturniids must wander back and forth, depending on the dryness, windiness, wetness, sunniness, etc., of the year. Something is stopping these breeding populations from moving gradually westward into Santa Rosa.

There are impediments to two classes of organisms. First, when a mutant appears that can handle whatever are the more inimical conditions of Santa Rosa, why does it not survive and produce a slightly modified portion of the population that moves ever further into Santa Rosa? Second, just exactly what are the inimical aspects of Santa Rosa habitats that stop the stricly rainforest genotype from moving into Santa Rosa habitats?

Why not invasion by a slightly modified portion of the population? This is not an essay on population genetics and it is most convenient to fall back on the conventional explanation. The stricly rainforest form is on an adaptive peak. While a mutant may have a trait that works well in Santa Rosa, it is somehow disruptive to the rainforest adaptive peak, so much so that the hybrids have too low viability in *either* habitat. Lacking a geographic barrier between the dry forest and rainforest, a Santa Rosa population never differentiates. I am not convinced by this explanation, but this is not the place to dissect it and hypothesize some other process that impedes invasion by a population through its genetic modification.

What is inimical about Santa Rosa to rainforest saturniids?

This question is most easily divisible into two parts. First, there are the things wrong with the habitat that have nothing to do with the presence of the other saturniids. These are easily imagined and I will not dwell on them here: the climate or weather is wrong, food plants are missing or growing at the wrong density, seasonal timing cues are missing or misleading, growing season is the wrong length, carnivore pressure is too intense (though this has both a density-independent *and* density-dependent component, see section to follow), crypticity or aposematism of adults and immatures is out of focus, etc. If only these things were involved, then the numbers of saturniid species in Santa Rosa would be simply a matter of time and proximity to the rainforest source area, and would not involve density-dependent responses to the number of saturniid species or individuals already present.

For example, is the weather not an adequate barrier to invasion by rainforest saturniids? Certainly the rainy season is not itself inimical to rainforest saturniids; these animals are quite at home in high humidity and the same temperatures as occur in Santa Rosa. Furthermore, there is no hint that Santa Rosa is invaded each rainy season by rainforest saturniids which are them eliminated by the next dry season.

It is certain that a simple lack of particular species of foodplants is not the cause of the failure of rainforest saturniids to colonize Santa Rosa's habitats. Many of the rainforest species whose hosts are known are either highly polyphagous (with their host lists including Santa Rosa species), or are specialists on plant taxa that occur in Santa Rosa. For example, I have reared *Automeris phrynon,* a widespread rainforest *Automeris,* on Santa Rosa *Inga vera* (it eats at least one other species of *Inga* at one Costa Rican rainforest site (Marquis 1985) and it certainly occurs in the rainforest only 23 km from Santa Rosa, at Finca San Gabriel, 16 km ENE of Quebrada Grande in Guanacaste Province). There are at least three species of Lauraceae-eating *Copaxa* in the rainforests adjacent to Santa Rosa, yet only *Copaxa moinieri* feeds on Santa Rosa's common *Ocotea veraguensis* (Lauraceae). On the other hand, there is still the possibility that the distribution of chemically suitable hosts in space or time is inimical to potentially invasive species. Yes, *Ocotea veraguensis* is a common evergreen treelet in Santa Rosa, but is it as abundant as is the combination of *Ocotea, Nectandra* and other Lauraceae that support 3-4 species of *Copaxa* at most lowland Costa Rican rainforest sites? I suspect that the reply is yes.

Second, there is the question of how do the 30 species of resident saturniids in Santa Rosa influence or potentially make life more difficult for a potential invading saturniid. If a new species of saturniid, monophagous or polyphagous, were to invade Santa Rosa, there is virtually no chance that it would compete directly with the other species of saturniids present. Since the adults do not feed, again they cannot compete directly for resources. While a saturniid population at Santa Rosa can produce a defoliation event at long intervals (e.g., *Hylesia lineata,* Janzen 1984d) the caterpillars normally occur at sufficiently low density that the chance of significant direct competition for leaves among species is negligible. However, there are two conspicuous ways that allospecific saturniids may influence each other in a density-dependent manner.

1) **Interspecific mate interference.** On the basis of frequent positive electrophysiological responses of male saturniid antennae to allospecific as well as to conspecific pheromones (e.g., Priesner 1968), it would be easy to conclude that it is commonplace for congeneric species to respond to each other (and see Peigler and Williams 1984 for two recent cases of male saturniids responding to allopatric

allospecific female saturniids). However, there are also enough exceptions in Priesner's (1968) survey that it would also often be the case that a specific congeneric pair of species would not crossreact. In other words, one cannot automatically assume that a species of, for example, *Automeris* (five already in Santa Rosa) or *Rothschildia* (two already in Santa Rosa) would constitute a reproductive barrier to the invasion by a rainforest congeneric, though the possibility remains. However, in the case of *Rothschildia* there is no possibility of reproductive interference, since the species of rainforest *Rothschildia* that is missing from Santa Rosa, *R. orizaba,* is sympatric with Santa Rosa's *R. erycina* and *R. lebeau* throughout Costa Rica's lowland rainforests. Equally, three of Santa Rosa's five *Automeris (A. zugana, A. rubrescens, A. metzli)* are cosmopolitan and sympatric with six strictly rainforest species of *Automeris* in Costa Rica's rainforests; again, mating interference at Santa Rosa is an unlikely cause of the failure of those six strictly rainforest *Automeris* to invade. As for the numerous other possible invaders from the rainforest (at least 20 species of saturniids), the same logic applies. I think it highly unlikely that interspecific mate interference has anything to do with the failure of rainforest saturniids to invade Santa Rosa.

2) **Shared carnivores.** When a new species of saturniid attempts to breed at Santa Rosa, its larvae encounter two overlapping yet ecologically distinctive sets of carnivores. First, there are those that primarily or only parasitize (parasitoidize) saturniids; in this group strong reciprocal density-dependent responses to both individuals and species richness of saturniids are possible. Second, there are those (parasites and predators) that may be a severe threat to saturniid larvae but whose populations are sustained by a much broader food base; in this group, responses are unlikely to be reciprocally density-dependent. They may make life very difficult for the invading saturniid, but the presence of 30 other species is irrelevant (see below).

With the first group, the truly monophagous species of carnivores (parasitoids) are not an immediate threat to the incoming saturniid. However, some that are monophagous in Santa Rosa may become diphagous in ecological time if a closely related saturniid moves into the habitat. For example, the single species of *Enicospilus* (Ichneumonidae) (Fig. 4) that is monophagous on *Rothschildia lebeau* caterpillars at Santa Rosa (it is so monophagous that it even ignores *Rothschildia erycina* caterpillars that are feeding on the same host with *R. lebeau,* or *R. erycina* caterpillars are immune to it) might well attack the very similar caterpillar of *Rothschildia orizaba.* As mentioned earlier, *R. orizaba* is a common member of the rainforest saturniid array just 10-15 km to the east of Santa Rosa, and two waif male *R. orizaba* have been encountered *in Santa Rosa. Being* larger and probably taking longer to develop as a larva, *R. orizaba* might well find that it cannot survive at the density of *Enicospilus* that is tolerated by *R. lebeau.* The *Enicospilus* population maintained by the *R. lebeau* population in Santa Rosa is certainly potentially part of the ecological barrier to the addition of *R. orizaba* as the 31st breeding saturniid in Santa Rosa, but it is probably not a barrier to invasion by the other saturniids in the nearby rainforest. Likewise, if a second species of *Copaxa* should enter the Park and oviposit on *Ocotea,* its larvae might well be attacked by the single species of *Enicospilus* that is monophagous on *Copaxa moinieri* in Santa Rosa. The same potential interaction applies to *Hylesis lineata* and its single species of apparently monophagous *Enicospilus.*

Turning to slightly more polyphagous carnivores, there are those whose primary larval resource base is still saturniids. For example, there is an apparently single species of *Belvosia* tachinid fly that parasitizes at least five species of hemileucine, ceratocampine and saturniine saturniid caterpillars in Santa Rosa. Such an animal might well be a sufficiently severe parasitoid to prevent entry by a 31st rainforest species of saturniid. The addition of each new usable species of saturniid to Santa Rosa makes life that much better for such a tachinid, and therefore renders it an ever more severe barrier to entry by yet one more saturniid. The same kinds of statements apply to other species of tachinids, ichneumonids and braconids in Santa Rosa that are polyphagous within the saturniids.

Moving on to ever more generalist parasitoids (and diseases and other carnivores), the height of the ceiling to saturniid invasion is one that is ever more insensitive to the number that are already there. Of the truly generalist carnivores, the vertebrates are the best known. However, there are also bugs, social wasps, ants, scorpions, spiders and beetles that constitute a severe threat. These carnivores – monkeys, birds, coatis, mice, rats, armadillos, peccaries, possums, and many species of invertebrates – exist on a very broad resource base, yet may of course also act as temporary specialists by concentrating their foraging on a particularily susceptible or abundant saturniid. However, its is unlikely that the addition of a 31st species of saturniid to Santa Rosa will increase the intensity of challenge by these carnivores to a level such that the number of resident saturniids falls again to 30 species. The addition of a 31st saturniid species then blurs into the general problem of what prevents the addition of the 2761st species of moth to Santa Rosa. Viewed in this more global manner, saturniids do have the property of being large (and potentially conspicuos and worth searching for by generalist carnivores), having long caterpillar life spans (1-2 months), and having slow population growth rates (1-2 generations per rainy season as opposed to potentially 3-5 per rainy season for a small moth). All of these are traits that should make the 31st saturniid harder than the average moth to introduce as the 2761st moth species in a system with a rich, intense and dense carnivore fauna.

But saturniid specialist and generalist carnivores exist in the rainforest to the east of Santa Rosa, and each species of rainforest saturniid has long ago proven that it can persist in their presence. Is there anything different about the Santa Rosa carnivore challenge? Yes. The seasonal cycle of carnivore intensity is clearly different at Santa Rosa than at a rainforest site. The early rainy season at Santa Rosa, when the first generation of saturniid larvae occurs, seems optimal from the caterpillar viewpoint. The parasitoids are only those that survived the caterpillar-free and harsh dry season, breeding bird density is only starting its rainy season increase, foliage is new and therefore minimally uncontaminated by infectious disease pathogens, and caterpillar density is maximal which in turn leads to maximal carnivore satiation. At this time, the invading saturniid should have the highest chance of a successful generation (and I will later argue that this is what the incoming migratory sphingids are doing).

However, by the end of the first generation (late June through August), Santa Rosa has its highest peak of carnivores, a peak that diminishes only as they starve or out-migrate. At least a portion of each of the Santa Rosa saturniid populations survives this period by being dormant as pupae (and some of these stay dormant until the beginning of the next year's rainy season). Other species must survive it by attaining such a high density with the firest generation that the survivors of the second generation maintain the population until the next year's rainy season. It is quite possible that the incoming 31st Santa Rosa saturniid species will either attempt continuous generations (as they apparently do in the rainforest) or always start at an initial density so low that the first generation is not big enough to produce a big enough second generation to survive the second half of the rainy season. From this viewpoint, 25 of the 30 saturniids at Santa Rosa are simply that set of rainforest species that was able to move in and survive this peak of carnivory. If the peak of carnivores is made up of species that do not respond in any reciprocal density-dependent manner to an increase in saturniid species richness at Santa Rosa, the number 25 is a simple result of how many rainforest species were available to colonize. On the other hand, if saturniid specialists, such as the *Belvosia* tachinid mentioned earlier, are an important part of the carnivore peak (and I think they are), then the number 25 may well represent some sort of density-dependent ecological ceiling. Reality probably lies somewhere in between, and also varies from saturniid taxon to taxon.

In summary, it seems clear that the Santa Rosa saturniid species richness is determined by both internal ecological density-dependent processes and the availability of potential colonists. Were an African cosmopolitan saturniid introduced to Costa Rica, it would not be surprising to see it spread into Santa Rosa. Likewise, it would not be surprising to see it fail to spread into Santa Rosa. Also, if it invaded, it would not be surprising to see its presence either raise the number of breeding species to 31 or result in the elimination of a previous resident. Whether Santa Rosa is ecologically saturated with saturniid species can only be determined experimentally, and will require an answer in stochastic terms summed over many species. The outcome of the experiments will hinge on the specific traits of the experimentally introduced species.

The Santa Rosa sphingids

Many aspects of the biogeography of Santa Rosa sphingids (Table 2) are similar to those of the saturniids, but there are many important details that differ. The most central are that sphingid adults 1) feed and therefore live a long time (many weeks to months), giving the adults much more time for more kinds of resource harvest than are available to saturniids, and 2) are often highly migratory (as well as locally mobile) in both sexes. Discussion of Santa Rosa sphingid species richness and other similar biogeographic questions demands a more global view than is the case with saturniids. An undifferentiated list of the sphingids in the Park is in fact at least three lists with different ecological processes determining the length of each. Furthermore, within the list of breeding residents, there are two very different ways to use Santa Rosa: migrants and year-round residents. These different lists have long been recognized by bird biologists, but are not traditionally part of insect faunistic lists (or of those of plant biologists, where waifs are often included in floristic lists), though butterfly biologists may include them (e.g., Shapiro 1974).

Where do they come from?

Just as for Santa Rosa saturniids, the 64 species of Santa Rosa breeding resident sphingids (Table 2) have a distinctive dryland faunal component. There are at least 12 species in this category: *Manduca dilucida, M. lanuginosa, M. barnesi, M. muscosa, Xylophanes turbata, X. maculator, X. juanita, Cautethia yucatana, Erinnyis yucatana, E. domingonis, Aleuron iphis, Phryxus caicus.* These dry forest species range into the dry lowlands of tropical Mexico (including the Yucatan Peninsula) as breeding populations and one has to go very far north from Santa Rosa before encountering other dry forest species that could be viewed as potential invaders with which to increase the list. However, there is one species in the upper margins of the Gulf of Nicoya (western Costa Rica, to the south of Santa Rosa) – *Manduca ochus* – that may also be a dry forest species and yet not find the right conditions or other requirements in Santa Rosa, since it is known in the Park only as a waif (Table 2).

However, just as with saturniids, the vast majority of the Santa Rosa sphingids are ecologically and geographically cosmopolitan species. At least 22 percent of the breeding resident species also breed in the United States (Table 2) (three are species that I collected as a child in Minnesota (45° N Latitude) as they visited petunia flowers: *Agrius cingulatus, Manduca sexta, Hyles lineata).* All 52 of Santa Rosa's resident cosmopolitan species are found in most lowland to mid-elevation rainforest sites in Costa Rica. However, in contrast with the saturniids, the cosmopolitan sphingids can be divided into two groups. There is a small group that appears to be present in the Park throughout the year as adults or larvae *(Amplypterus gannascus, A. ypsilon, Protambulyx strigilis, Hemeroplanes triptolemus, Pachylia ficus, Manduca florestan, Madoryx oiclus)*; it is not yet clear to what degree their pupae may also be seasonally dormant (if at all). There is then a much larger group of species that appear to arrive with the first rains, apparently from wetter parts of Costa Rica, have one or two generations during the first 2-4 months of the rainy season, and then leave as adults for wetter parts of the country where they probably have 1-2 generations before returning at the beginning of the next rainy season (Table 2). I will discuss their biology in greater detail below. (Incidentally, such a migratory pattern is probably responsible for at least part of the "seasonality" of rainforest sphingids, at least as measured by catches at lights.) Some of the species that are present as adults throughout the year also have migratory individuals (e.g. *Manduca florestan, Pachylia ficus*). Finally, there is a small set of species that has one or two generations in the rainy season and then many if not all of the pupae remain dormant in the litter 5-10 cm under ground until the next year's rainy season or at least for a substantial portion of the rainy season and following dry season: e.g., *Manduca dilucida, M. lefeburei, M. barnesi, M. lanuginosa, Xylophanes turbata.*

Another small set of species are rainforest species that appear to be actively probing Santa Rosa. These species are difficult to distinguish from waifs, but I define them as species that only in some years enter the Park and have (or attempt to have) at least one generation (Table 2: Occasional breeding residents). Perhaps the best examples are *Pachygonia drucei* and *Aleuron carinatum,* whose larvae eat the leaves of *Doliocarpus dentatus* (Dilleniaceae), a rainforest vine that occurs in a few wet sites in the Park. I believe that were the rainforest source area to be destroyed, these species would immediately disappear from the Park. As will be discussed below, this belief also extends to many of the breeding residents that regularly migrate into the Park.

Finally, there are the waifs (Table 2). As with the saturniids, all unambiguous waif sphingids come from the rainforests to the east of the Park. Waifs (e.g., *Protambulyx xanthus, Madoryx pluto, Manduca hannibal, Eumorpha triangulum, E. obliqua, Callionima parce, C. inuus, Xylophanes amadis)* appear at lights as singletons at very irregular intervals. They are common species at various Costa Rican rainforest sites. There is as yet no suggestion that Santa Rosa occasionally receives a portion of a large migratory flight headed elsewhere. However, *Enyo lugubris,* which has not yet been found breeding in the Park, appears in large numbers of both sexes in the early dry season and might be such an animal. Additionally, there are three dry forest sphingind species *Madoryx bubastus, Manduca ochus,* and *Dolbogene igualana* — that are poorly understood and might be dry forest waifs. *D. igualana* might even breed in Santa Rosa, (W. Haber, personal communication) and so I have placed it in the category of 'occasional breeding species'.

Migrant sphingids.

If a light is placed in one of the passes at 600-1800 m elevation in the north-south mountain chain (Cordillera de Guanacaste) separating Costa Rica's Pacific coastal dry forest lowlands from the rainforest on the Atlantic side, large numbers of lowland sphingids are often captured at that light (see Janzen 1984b for an example from the Talamanca mountain range immediately to the south of San José, Costa Rica). They are of both sexes, in strong contrast to the strong bias to males at lights in the lowland breeding grounds. They are always newly-eclosed (or at least, have unworn wings). The largest catches occur at the beginning and end of the dry season

(December, April-May). There is no doubt that they are moving from one major habitat type to the other. It is unknown for most species if they have a generation while on the rainforest side, but there are numerous reasons to suspect that they do. In all cases where their hosts are known, their host plant species or genera are present on both sides of Costa Rica. For example, *Isognathus rimosus* and *Pseudosphinx tetrio* are probably flying from coast to coast (150-plus km), since their sole host tree *Plumeria rubra* (Apocynaceae) – grows in Costa Rica only in the coastal regions on both sides of the country. Alternatively or additionally, the adults may be passing the dry season months as adults visiting flowers in evergreen forest areas; if this is the case, however, it is striking and odd that they leave Santa Rosa, since there is an abundance of dry season nectar-rich flowers in the dry forest.

Perigonia interupta is particularily instructive with respect to migration (this moth was included with its sibling *P. ilus* under the name *P. lusca* in Janzen 1984c). For a period of about a month around the start of the rains at Santa Rosa, large and moderately unworn individuals of this small sphingid appear at the lights. It oviposits on its two host plants in Santa Rosa *(Calycophyllum candidissimum* and *Guettarda macrosperma,* in the Rubiaceae) and the caterpillars are abundant during the month that follows. They pupate in the litter. In the laboratory, all adults eclose 2-3 weeks after they pupate in either wet or dry conditions, so I assume that adult eclosion is the same in nature. These adults weigh significantly less than did their parents and have shorter wings (Table 3). *P. interupta* then disappears from the Park (it is not encountered at lights or flowers, nor as caterpillars). Presumably it has left for the rainforest side of Costa Rica, where it is the common *Perigonia* taken at lights. When *P. interupta* reappears at the beginning of the next rainy season, the individuals are again large, demonstrating that it has had another generation in the meantime. *P. ilus* behaves as described for *P. interupta,* but has two generations in the rainy season in the Park before leaving, and the adults produced from the first generation of caterpillars in the Park do not appear to be smaller than are the incoming adults at the beginning of the rains.

At present there is no way to know if offspring of the migrant sphingids from Santa Rosa also return exactly to Santa Rosa the following year (extra-tropical migrant birds may return to the site of their birth cf. Whitcomb *et al* 1981, but they are not breeding on the tropical wintering ground). I doubt that an adult sphingid lives long enough to make the round trip. Most likely, the sphingids move back and forth over the shortest route, and then spread out in search of suitable habitat upon arrival. Such a pattern would, however, still lead to northern Costa Rican rainforest being primarily interdependent with northern Costa Rican dry forest rather than with all of Costa Rican dry forest.

By adding a migratory aspect to Santa Rosa sphingid biology, the picture is more occurate but more complicated than is obtained by treating Santa Rosa as a self-contained entity. These sphingids are like migrant birds in moving to a new habitat in which to produce young, but are unlike them (and monarch butterflies) in that they have one or more generations in each major habitat occupied. It is impossible to state firmly in which habitat a cosmopolitan sphingid evolved, or even if it should be thought of as having evolved in one or the other habitat. The carrying capacity of Santa Rosa for sphingids, as measured by species present, is very different in the dry season than the wet. It is not clear if the sphingids leave Santa Rosa during the second half of the rainy season and during the dry season because there is insufficient carnivore-free resource space, because they have never been able to evolve a morph that can survive the dry season as a dormant pupa (highly unlikely), or because their fitness is higher by having another generation in the rainforests than by waiting in the dry forest in reproductive or pupal dormancy until the next year. Even more puzzling is the question of why all of the lowland rainforest sphingid fauna does not migrate into Santa Rosa for a generation during the first half of the rainy season. It could well be that the more that leave the rainforest, the better life is for those that stay behind, creating an equilibrium number of non-migrants that is greater than zero.

Ceilings to sphingid species packing in Santa Rosa

More than half the breeding fauna of sphingids at Santa Rosa appears to be regularily migratory. This adds great confusion to the question of species packing and to what determines the ceilings to species richness.

Host plants.

Nothing about sphingid host-plant specificity suggests that the failure of at least 20 species of nearby rainforest sphingids to invade Santa Rosa and have a generation in the rainy season is due to the absence of particular species of host plants. All known larval hosts of Costa Rican rainforest sphingids occur in Santa Rosa or else Santa Rosa contains close relatives (the general case with sphingids, in contrast to saturniids, is that their species-rich host lists accumulated over a large geographic area are very low in generic– or family-level richness). Caterpillars of closely related sphingids most commonly feed on closely related or the same host plant species and most of the Costa Rican rainforest sphingids have close relatives that breed in Santa Rosa.

Just as is the case with Santa Rosa saturniids, there is nothing about the way that the sphingid caterpillars consume their host plants to suggest that allospecific caterpillars affect each other through direct competition for leaves or that an invader would encounter such direct competition. Even in the rare and widely-spaced cases of severe host plant defoliation (e.g., *Xylophanes turbata* on *Psychotria microdon,* Janzen 1982; *Aellopos titan* on *Randia subcordata* and *R. karstenii,* Janzen 1985b), it seems unlikely that one species would have enough of a competitive edge so as to annihilate the other during a defoliation event that is not annual, that lasts only one generation (the usual duration, e.g., Janzen 1985b) and that does not defoliate all members of the host population.

While it seems reasonable that sphingids might competitively interact over floral resources for adults, many species of flowers of the types visited by sphingids are superabundant. It is commonplace for Santa Rosa sphingid flowers (e.g., *Alibertia edulis, Coutarea hexandra, Exostema mexicanum, Chomelia spinosa, Luhea speciosa, Calliandra emarginata, Erythroxylum havanense*) to produce abundant nectar yet go for many nights with very little visitation. Rather than interspecific competition being a problem for adult sphingids, the enormous number of flowers never visited yet rich in nectar leads one to feel that perhaps it is the plants that are really feeling the effects of competition for pollinators rather than that the sphingids are often competing for flower nectar.

Carnivores.

While there appears to be virtually no saturniid-sphingid interchange of parasitoids, the Santa Rosa sphingid fauna does support a set of monophagous to moderately polyphagous parasitoids of sphingids that could have the same effect on an invading species as was postulated earlier for the saturniids. *Thyreodon atriventris* (Ichneumonidae) parasitizes at least 4 species of Santa Rosa sphingids (and probably many more) and two slightly smaller undescribed species of *Thyreodon* have a sphingid host list as long and but not overlapping with that of *T. atriventris.* The same several species of tachinid flies are repeatedly reared from some 15 species of *Manduca, Erinnyis, Pachylia* and *Pachylioides.* One distinctive species of braconid has been reared from at least *Erinnyis ello, E. alope, E. crameri, E. oenotrus, Manduca lefeburei, M. occulta, M. dilucida, M. lanuginosa, M. florestan, Pachylioides resumens* and other moderately large sphingids. One set of relatively small sphingids *(Enyo ocypete, Aellopos fadus, Eupyrrhoglossum sagra, Perigonia* spp.) is heavily attacked by what appears to be one species of *Belvosia* tachinid, while another species of *Belvosia* attacks the larger *Manduca* larvae. All of these parasitoids constitute a multi-talented body of killers. Each new sphingid species that invades Santa Rosa increases their omnipresence, versatility and biomass. Of course, the increase may result in the decimation and/or extinction of a sphingid that was there previously, rather than eliminate the invader; whatever occurs, the response should be sensitive to the number of sphingid species at the site, in as much as an increased number of sphingid species increases the chance that in any given year at least one species will be abundant enough for parasitoid survival. Worse, from the sphingid viewpoint, the more species of susceptible sphingids the greater the chance that one will be abundant enough in a given year to create a large pulse of parasitoids that will kill an exceptional number of hosts of other species as it starves back to a more usual density.

The same suite of more generalist invertebrate and vertebrate carnivores that attack the 30 species of Santa Rosa's breeding saturniids are a threat to the sphingids. As mentioned earlier, these carnivores are supported by a much larger resource base than just the sphingids and saturniids, and probably generate an intensity of mortality that is relatively independent of sphingid species richness. Each new incoming sphingid species has to be able to survive this carnivore threat irrespective of the other moths. However this observation should not be construed to suggest that, from the viewpoint of each species of sphingid, they are always density-independent predators. Many of these predators do respond to local increases in large caterpillars or pupae by searching more often and more carefully at the point of high density.

Just as with the saturniids, the strictly rainforest sphingids demonstrate by their very presence that they can tolerate an impressive array of carnivores. However, I suspect that Santa Rosa is substantially freer of carnivores in the beginning of the rainy season than is the rainforest, and therefore is the right place for a sphingid to go, if it can, to have a generation; the question then becomes why don't all of the rainforest species do it? I suspect that the majority of the Santa Rosa sphingids leave the dry forest after the first or second generation because the build up of carnivores on the caterpillar generations (and on other food) in the first half of the rainy season produces a challenge that is too severe. Migration is here viewed as analogous to the behavior of many Santa Rosa saturniids which become dormant as pupae after only one or two rainy season generations. Other sphingids, such as *Manduca dilucida* and *M. lanuginosa,* act like a saturniid in "leaving" by remaining as pupae 10-15 cm below the soil surface. Only a minute fauna of sphingid caterpillars is in Santa Rosa during the second half of the rainy season and in the following dry season. In a certain sense, many sphingids move in and use Santa Rosa resources temporarily while the saturniids somehow tolerate the habitat throughout the year. Viewed in this manner, the ceiling to species richness of sphingids in Santa Rosa will certainly be dependent on the size and proximity of rainforest sphingid faunas and their habitats to the dry forest, as well as on the carnivore dynamics within the dry forest.

More globally

It is apparent that somewhat different processes determine the carrying capacity of a place or habitat for saturniid and sphingid numbers and species richness. Both taxa are confronted with inclement physical conditions and carnivores that are shared to various degrees. However, Santa Rosa is close enough to evergreen refuges so that sphingid migratory abilities give them a chance to use the Park as seasonal visitors. Furthermore, if a local event eliminates a generation of a migratory sphingid species, it is likely to be replaced through normal immigration in the following year. A saturniid population can only be replaced through gradual expansive movements by females from the margin of a breeding population.

Virtually all of the dry forest (or its remnants) of lowland Mexico and Mesoamerica lie within 200 km of evergreen forest (or its remnants), suggesting that migration of sphingids should be an important part of moth biology wherever dry forest is found. Perhaps the most dramatic biogeographic manifestation of sphingid mobility and migratory behavior is the fact that while the Caribbean Islands are rich in sphingid species (e.g., Schreiber 1978), there is only one species of saturniid, a hemileucine, on a Caribbean island (Hispaniola; C. Lemaire, personal communication). (I exclude Trinidad, which is just a peninsula tip recently cut off from the mainland.).

Looking at the Neotropics more globally, it is easy to predict that the cumulative species/area curves for sphingids and saturniids will be very different in shape and asymptote (Fig. 5). By virtue of their mobility, species of sphingids will be able to occupy (use) more habitats; the average habitat will therefore be occupied by more species of sphingids than (the less mobile and short-lived) saturniids. While this may lead also to more rapid and more dramatic speciation in saturniids than in sphingids, there are quite enough species of rainforest saturniids waiting in the wings (the nearby rainforest) that simple lack of available species cannot solely be blamed for the absolute number of species at Santa Rosa. Brown (1982:461) has reached a similar conclusion for three species groups of closely related butterflies, in an analysis of all of the Neotropics. If there were a process somewhere that was generating species of saturniids and sphingids that were adapted to dry forest, and then introducing them into the Pacific coastal lowlands, could Santa Rosa's species richness in these taxa still rise? There is absolutely no way to know without doing the experiment. I would opt, however, for a "yes" reply.

Implications for conservation

Saturniids, in their relatively sedentary breeding populations, may well initially respond little to the agronomic insularization of Santa Rosa, provided that the Park is large enough to maintain a breeding population in normal years. And it does appear large enough for that. However, as is the case with many kinds of organisms, we can predict that there will be periodic catastrophic events in the Park, ranging from runs of exceptionally dry (or wet) years to disease epidemics to overflow of agrochemicals and biocontrol agents from croplands. Since there is no longer adjacent dry forest from which the saturniid population can reinvade Santa Rosa, such a local extinction will be forever. The subsequent ripple effect on the surviving saturniids and their monophagous to narrowly polyphagous parasitoids is potentially both negative and positive.

It should be pointed out, however, that at least a few saturniid species will at least seem to persist for a substantial period in fields and pastureland because their larvae eat the leaves of trees left in fencerows and along creeks (e.g., *Caio undilinea, Arsenura armida,* and *Titaea tamerlan* on *Bombacopsis quinatum; Syssphinx molina* on *Pithecellobium saman; Syssphinx mexicana* on *Acacia collinsii; Adeloneivaia isara* on *Lysiloma* spp.). However, these species will disappear abruptly as the large old adult trees senesce (such fence-row trees generally do not reproduce, but rather are remnants from times when timber and space harvest was less severe). Extinction of the moths following the loss of the large trees will be further hastened by the fact that even if there are juvenile trees present, these species of moths do not have the behavior of ovipositing on them. However, even their present day presence is problematical. These moths are much more abundant on the host trees in pastures that are also within a few kilometers of the Park or of small forest remants than they are in very large pasture sites. This suggests that the "population" on scattered pasture trees may in fact be maintained by immigration of females from nearby forest rather than be self-sustaining.

Only *Rothschildia lebeau, Automeris io, A. rubrescens,* and *A. zugana* of the Santa Rosa fauna have the appropriate host plant preferences and ovipositional behavior to allow survival in the low woody secondary succession along fencerows. Their persistence in farmland is also aided by the fact that, in contrast to sphingids, adult saturniids do not require floral resources.

Finally, there should be coyotes in the moth world. Just as the coyote has spread ghroughout Pacific coastal Costa Rica and Panama following deforestation (eg., Vaughan 1983), some moths may become more common and widespread with deforestation. This requires at the least that their herb or shrub host plants grow in fencerows, open pastures or other early secondary successional sites. Among saturniids and sphingids, these moth species might be those that feed on fast-growing secondary successional plants. *Syssphinx mexicana* (Saturniidae), monophagous on ant-cacacias (*Acacia collinsii, Acacia cornigera*) might be expected to persist in pasture and farmland cut from dry forest, since these shrubs or treelets become abundant with certain kinds of land use; however, this moth is almost extinct in deforested Guanacaste and I suspect that even though its host plants are common in brushy pastures, the climate differences (between the Park and its surroundings) or new micro-geographic patterns of the hosts have eliminated it. In the Park, *S. mexicana* larvae are found only on ant-acacias growing in or adjacent to forest, rather than on the isolated acacias in open abandoned pasture.

With sphingids the story is quite different from that of saturniids. Each year that the migrant sphingids return from the rainforest side of Costa Rica, they find the dry forest area with host plants for larvae and adults to be reduced in area. This may result in a decrease or increase in density of particular sphingids at Santa Rosa, depending on the ability of each species of sphingid to locate ever more scattered forest. However, it is apparent that even if Santa Rosa and other small patches can sustain an increased density of migrant sphingids, overall there is no way they can generate as many moths as originally did all of the dry forest lowlands of the Pacific coast of Costa Rica. Similarily, Whitcomb *et al* (1981) found that migrant birds, returning to find their forest of origin destroyed, moved into nearby forest (raising density) but then the density declined in subsequent years, apparently due to insufficient bird production.

As the density of migrants to the rainforest declines, so must the numbers decline that return at the beginning of the next rainy season. This decline is exacerbated by the nearly total elimination of the Costa Rican wet forest areas that the sphingids migrate to (only several small patches of Atlantic lowland rainforest still exist in Costa Rica). This downward spiral can have no final effect other than to move the sphingid density closer to a level where a chance severe perturbation will extinguish a species. Worse, it is clear that the elimination of Guanacaste's dry forests will have a heavy effect on Costa Rica's rainforests through decimation or extinction of major pollinators such as those migrant sphingids that ecologically originate on the dry side of the country.

The Costa Rican national parks and other preserved areas are of course islands, but these islands have a connectedness. Furthermore, this connectedness appears to exist for much more than just a few species of sphinx moths: there appears to be inter-habitat seasonal migration by euglossine bees (Janzen 1981, Janzen *et al* 1982), butterflies (W.A. Haber, personal communication; P.J. DeVries, personal communication; F.G. Stiles, personal communication); tachinid flies (unpublished inference from the present study); birds (F.G. Stiles, personal communication; DHJ, personal observation); and noctuid moths (unpublished observations from the present study).

This comparison of saturniids and sphingids is particularly relevant to Diamond's (1984) generalization that "species differences in persistance today cannot be interpreted unequivocally in terms of differences in resistance to extinction: they may also mean differences in ability to recolonize.". Saturniids will recolonize only from adjacent populations, and even that will occur only slowly through the movement of relatively sedentary females. Sphingids should recolonize rapidly (assuming a source area), if they are of the species that seasonally migrate. However, even if recolonized, their densities – and hence ecological effects – may well be grossly different from those originally at the site. It will be most instructive, though depressing, to track the relative changes in saturniid and sphingid density and species richness in Brazilian flatland rainforest as the experimental forest islands (Lovejoy *et al* 1984) reach their ecological equilibria and the source area forest recedes ever further from them.

Resumen

El Parque Nacional Santa Rosa es arbitrariamente definido como una porción de bosque seco de 108 km^2 de tamaño aproximado, situado al noroeste en las tierras bajas del Pacífico de Costa Rica. Hay 30 especies de mariposas nocturnas de la familia Saturniidae que se reproducen en el Parque (y 5 especies que entran como desorientadas, y 64 especies de la familia Sphingidae que realmente se reproducen en el Parque. También ocurren 10 especies de Sphingidae que ocasionalmente se reproducen en el Parque, y hay por lo menos 9 especies que ocurren en el Parque como desorientadas (83 especies en total). Hay una especie endémica de la familia Saturniidae *(Schausiella santarosensis)* y no hay especies endémicas de la familia Sphingidae. En adición, casi todos los Saturniidae y los Sphingidae del Parque tienen distribuciones muy amplias con respecto a su geografía y ecología. Los Saturniidae dormitan durante la estación seca (seis meses) y todos sobreviven al tiempo seco dentro del Parque. Más de la mitad de los Sphingidae migran fuera del Parque durante la estación seca y parece que ellos se reproducen en estos meses

en las partes más lluviosas de Costa Rica. Esta migración es parte integral de la interdependencia de Santa Rosa con las otras partes de Costa Rica y viceversa.

¿Qué determina el número de especies de Saturniidae y Sphingidae en Santa Rosa? El Parque no está aislado. No existen murallas que limiten la entrada a las especies de mariposas nocturnas que se reproducen únicamente en los bosques lluviosos, solamente a 10 ó 15 km al este del Parque. Este bosque lluvioso es ocupado por lo menos por 25 especies de Saturniidae y Sphingidae que también se reproducen en Santa Rosa. También ¿por qué los Saturniidae y Sphingidae del bosque lluvioso no entran al Parque para reproducirse durante la estación lluviosa? No hay ni una evidencia que la competencia directa esté previniendo la entrada de los 31 Saturniidae o los 65 Sphingidae a Santa Rosa. Igualmente parece que hay suficientes especies de plantas de las especies correctas para cualquier especie de Saturniidae o Sphingidae que empieza a invadir Santa Rosa. Sin embargo, Santa Rosa tiene un grupo formidable de depredadores y parasitoides que comen larvas de Saturniidae y Sphingidae. Por un lado,· este grupo es lo suficientemente reducido por la estación seca, los Saturniidae y Sphingidae pueden producir de 1 a 2 generaciones. Es muy probable que el nivel bajo de animales carnívoros, es la causa de la migración de los Sphingidae al Parque cuando empieza las lluvias. Por otra parte, los carnívoros contienen suficientes especialistas y semi-especialistas parasitoides para proveer la mortalidad de la forma "desntiy-dependent" y pueden regular el número de especies de Saturniidae y Sphingidae que ocurren en Santa Rosa. Hay numerosas especies de parasitoides que pueden intensificar su depredación si hay aumento en el número de Saturniidae of Sphingidae que se reproduce en Santa Rosa. Esta intensificación puede prevenir la entrada del emigrante o eliminar su residente.

Santa Rosa está en un estado de interdependencia con los otros habitats en Costa Rica, incluyendo el bosque seco que (estaba) en la vecindad. Si, por ejmplo, los bosques lluviosos de Costa Rica no existen más para generar y recibir emigrantes de Santa Rosa, habrá impactos del segundo y tercer orden en la fauna residente y en la estructura ecológica del Parque.

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Table 1. Checklist and geographic distribution of the Saturniidae of Santa Rosa National Park, Northwestern Costa Rica (0-350 m elevation). [1/]

Residents:	**Date described**[2/]	**Type locality**[3/]	**Range**[4/]	**Costa Rican habitat**[1/][5/]
Saturniinae				
Copaxa moinieri Lemaire	1974	Panama	Costa Rica and Panama	R + D
Rothschildia lebeau (Guerin-Meneville)	1868	Venezuela	Texas to Venezuela and Peru	R + D
Rothschildia erycina (Shaw)	1796	Neotropics	Mexico to Amazonia and Bolivia	R + D
Arsenurinae				
Arsenura armida (Cramer)	1779	Surinam	Mexico to southern Brazil and Bolivia	R + D
Caio championi (Druce)	1886	Panama	Mexico to Venezuela and Colombia	R + D
Copiopteryx semiramis (Cramer)	1775	Surinam	Mexico to southern Brazil and Bolivia	R + D
Dysdaemonia boreas (Cramer)	1775	"West Indies" (= Neotropics)	Mexico to Amazonia and Bolivia	R + D
Titaea tamerlan (Maasen)	1869	Brazil	Mexico to southern Brazil and Bolivia	R + D
Ceratocampinae				
Adeloneivaia isara (Dognin)	1905	El Salvador	Northern Mexico to Costa Rica	D

cont...

Table 1. (cont...)

Residents:	Date described[2]	Type locality[3]	Range[4]	Costa Rican habitat[1] [5]
Citheronia bellavista Draudt	1930	Colombia	Nicaragua to Venezuela and Ecuador	R + D
Citheronia lobesis W. Rothschild	1907	Costa Rica	Costa Rica and Venezuela and Colombia	D
Eacles imperialis (Drury)	1773	USA	Canada to Argentina and Brazil	R + D
Othorene purpurascens (Schaus)	1905	French Guiana	Mexico to southern Brazil and Peru	R + D
Othorene verana (Schaus)	1900	Mexico	Northern Mexico to Panama	R + D
Ptiloscola dargei Lemaire	1971	Nicaragua	Mexico to Panama, Ecuador	R + D
Schausiella santarosensis (Lemaire)	1982	Costa Rica	Costa Rica	R + D
Syssphinx colla (Dyar)[6]	1907	Mexico	Mexico to Panama	R + D
Syssphinx mexicana (Boisduval)[6]	1872	Mexico	Mexico to Costa Rica	D
Syssphinx molina (Cramer)	1780	Surinam	Mexico to Argentina and Bolivia	R + D
Syssphinx quadrilineata (Grote and Robinson)[6]	1867	Mexico	Mexico to Venezuela and Ecuador	R + D
Hemileucinae				
Automeris io (Fabricius)	1775	USA	Canada to Costa Rica	R + D
Automeris metzli (Salle)	1853	Mexico	Mexico to Venezuela and Ecuador	R + D
Automeris rubrescens (Walker)	1855	Guatemala	Mexico to Costa Rica	R + D
Automeris zugana Druce	1886	Panama	Costa Rica to Ecuador	R + D
Automeris zurobara Druce	1886	Panama	Mexico to Venezuela and Panama	D

cont...

Table 1. (cont...)

Residents:	Date described 2/	Type locality 3/	Range 4/	Costa Rican habitat 1/ 5/
Dirphia avia (Stoll)	1780	Surinam	Nicaragua to southern Brazil and Bolivia	R + D
Hylesia dalina Schaus	1911	Costa Rica	Mexico to Ecuador	R + D
Hylesia lineata Druce	1886	Costa Rica	Mexico to Panama	R + D
Molippa nibasa Maassen	1885	Mexico	Mexico to Argentina and Bolivia	R + D
Periphoba arcaei (Druce)	1886	Panama	Mexico to Panama	R + D
Waifs:				
Saturniinae				
Rothschildia orizaba (Westwood)	1854	Mexico	Mexico to Venezuela and Peru	R
Ceratocampinae				
Adeloneivaia jason (Boisduval)	1872	Mexico	Mexico to southern Brazil and Bolivia	R
Hemileucinae				
Automeris hamata Schaus	1906	Costa Rica	Mexico to southern Brazil and Bolivia	R
Hylesia hamata Schaus	1911	Costa Rica	Costa Rica	R
Hylesia umbrata Schaus	1911	Costa Rica	Costa Rica to Peru and Brazil	R

1/ Based on Janzen (1982) and subsequent collections by D.H. Janzen and W. Hallwachs in Costa Rica.

2/ Date of publication of name; in many cases the moth was collected even earlier but not recognized as a new species at the time.

3/ Obtained from C. Lemaire's unpublished checklist of the Saturniidae of the New World south of the United States – Mexico border.

4/ Derived from Lemaire (1971-1976, 1978, 1980, 1987; personal communication).

5/ R = rainforest; D = dry forest. With reference to habitats below 500 m elevation.

6/ Listed as *Sphingicampa* in Janzen (1982), but *Syssphinx* in Lemaire (1985).

Table 2. Checklist[1/] and range of the Sphingidae of Santa Rosa National Park, northwestern Costa Rica.

Regular breeding residents[2/]	Apparently migratory	Range[3/]	Range in Costa Rica[4/]
Agrius cingulatus (F.)	+	central US to Chile and Argentina, Caribbean	R + D
Aellopos clavipes R. & J.)	+	southern US to Argentina, Caribbean	R(?)+ D
Aellopos fadus (Cram.)	+	southern US to Paraguay, Caribbean	R(?)+ D
Aellopos titan (Cram.)	+	eastern US to Argentina, Caribbean	R + D
Aleuron iphis (Walker)	+	Mexico to southern Brazil,	D
Amplypterus ypsilon R. & J.		Mexico to Colombia and northern Brazil	R + D
Amplypterus gannascus (Stoll)		Mexico to Argentina,	R + D
Callionima falcifera (Gehlen)		Mexico to Brazil	R + D
Cautethia spuria (Bdv.)		Texas to Costa Rica	R(?)+ D
Cautethia yucatana Hy. Edwards		Mexico to Costa Rica	D
Cocytius duponchel (Poey)	+	Mexico to Argentina, Caribbean	R + D
Cocytius lucifer R. & J.	+	Mexico to Brazil	R + D
Enyo lugubris (L.)	+	eastern US to Argentina, Caribbean	R + D
Enyo ocypete (L.)	+	Mexico to Argentina, Caribbean	R + D
Erinnyis alope (Drury)	+	southern US to Argentina, Caribbean	R + D
Erinnyis crameri (Schaus)	+	southern US to Argentina, Caribbean	R + D
Erinnyis domingonis (Butl.)	+	southern US to Argentina, Caribbean	D
Erinnyis ello (L.)	+	southern and southwestern US to Argentina, Caribbean	R + D
Erinnyis lassauxii (Bdv.)	+	southern US to Argentina, Caribbean	R + D
Erinnyis obscura (F.)	+	southern and southwestern US to Argentina, Caribbean	R + D
Erinnyis oenotrus (Cram.)	+	southern US to Argentina, Caribbean	R + D
Erinnyis yucatana (Druce)		Arizona to Costa Rica	D
Eumorpha anchemola (Cram.)	+	Mexico to Argentina	R + D
Eumorpha labruscae (L.)	+	southern US to Chile and Argentina, Caribbean	R + D
Eumorpha satellitia (L.)	+	Mexico to Argentina,	R + D

cont...

Table 2. (cont...)

Regular breeding residents[2/]	Apparently migratory	Range[3/]	Range in Costa Rica[4/]
Eumorpha vitis (L.)	+	eastern US to Argentina, Caribbean	R + D
Eupyrrhoglossum sagra (Poey)	+	Mexico to Paraguay, Caribbean	R + D
Hemeroplanes triptolemus (Cram.)		Mexico to Brazil	R(?)+ D
Isognathus rimosus (Grote)	+	Mexico to Brazil, Caribbean	R + D
Madoryx oiclus (Cram.)		Mexico to Argentina, Caribbean	R + D
Manduca barnesi (Clark)		Mexico to Costa Rica	D
Manduca corallina (Druce)		Mexico to Venezuela	R + D
Manduca dilucida (Hy. Edwards)		Mexico to Venezuela	D
Manduca florestan (Cramer)	+ (?)	Arizona to Argentina	R + D
Manduca lanuginosa (Hy. Edwards)		Mexico to Venezuela and Ecuador	D
Manduca lefeburei (Guer.)		Mexico to Paraguay	R(?)+ D
Manduca muscosa (R. & J.)		Arizona to Costa Rica	D
Manduca occulta (R. & J.)		Arizona to Costa Rica	R + D
Manduca rustica (F.)	+ (?)	Southwestern and eastern US to Argentina and Chile, Caribbean	R + D
Neococytius cluentius (Cram.)	+	Mexico to Argentina, Caribbean	R + D
Nyceryx coffeae (Walker)	+	Florida to Brazil	R + D
Nyceryx riscus (Schaus)		Mexico to Paraguay	R(?)+ D
Pachylia ficus (L.)		southern US to Argentina and Chile, Caribbean	R + D
Pachylia syces Hbn.)		Mexico to Argentina, Caribbean	R + D
Pachylioides resumens (Walker)	+	Mexico to Argentina, Caribbean	R + D
Perigonia ilus Bdv.[5/]	+	Mexico to Brazil	R + D
Perigonia interupta Walker[5/]	+	Mexico to Brazil	R + D
Phryxus caicus (Cram.)		Florida to Argentina, Caribbean	D
Protambulyx strigilis (L.)		Florida to Argentina, Caribbean	R + D
Pseudosphinx tetrio (L.)	+	southern US to Argentina Chile, Caribbean	R + D
Sphinx merops Bdv.		Mexico to Ecuador	R + D
Unzela japix (Cram.)	+	Mexico to Brazil	R + D
Unzela pronoe (Druce)	+	Mexico to Brazil	R + D
Xylophanes anubus (Cram.)	+	Mexico to Paraguay	R + D
Xylophanes ceratomioides (G. & R.)	+	Mexico to Paraguay	R + D
Xylophanes chiron Dry.	+	Mexico to Paraguay, Caribbean	R + D

cont...

Table 2. (cont...)

Regular breeding residents[2/]	Apparently migratory	Range[3/]	Range in Costa Rica[4/]
Xylophanes juanita R. & J.		Mexico to Costa Rica	D
Xylophanes libya (Druce)	+	Mexico to Bolivia and Brazil	R + D
Xylophanes maculator (Bvd.)	+	Mexico to Ecuador and Venezuela	D
Xylophanes pluto (F.)	+	southern US to Argentina, Caribbean	R + D
Xylophanes porcus (Hbn.)	+	Mexico to Paraguay, Caribbean	R + D
Xylophanes tersa (L.)	+	eastern US to Chile and Argentina, Caribean	R + D
Xylophanes turbata (Hy. Edwards)	+	Mexico to Venezuela	D
Xylophanes tyndarus (Bvd.)	+	Mexico to Argentina	R + D
Occasional breeding residents[6/]			
Aleuron carinatum (Walk.)	+	Mexico to Brazil	R + D
Aleuron chloroptera (Perty)	+	Mexico to Argentina	R + D
Cocytius antaeus (Drury)	+	Florida to Argentina Caribbean	R + D
Dolbogene igualana (Schaus)		Mexico to Costa Rica	D
Enyo gorgon (Cramer)	+	Florida to Argentina	R + D
Eumorpha fasciata (Sulz.)		eastern US to Argentina, Caribbean	R + D
Hyles lineata (F.)	+	Canada to Chile and Argentina, Caribbean	R(?) + D
Manduca hannibal (Cram.)		Mexico to Paraguay	R + D
Manduca sexta (L.)		Canada to Chile and Argentina, Caribbean	R + D
Pachygonia drucei R. & J.	+	Mexico to Ecuador	R + D
Waifs[7/]			
Callionima inuus (R. & J.)		Mexico to Argentina	R
Callionima parce (F.)		southern US to Argentina Caribbean	R
Eumorpha obliqua (R. & J.)		Mexico to Brazil, Caribbean	R
Eumorpha triangulum (R. & J.)		southern US to Bolivia and Colombia	R
Madoryx pluto (Cramer)		Mexico to Argentina	R
Madoryx bubastus (Cramer)		Mexico to Paraguay, Caribbean	D (?)
Manduca ochus (Klug)		Guatemala to Paraguay	D
Protambulyx xanthus R. & J.		Costa Rica	R
Xylophanes amadis (Stoll)		Mexico to Bolivia	R

cont...

Table 2. (cont...)

1/ Based on collections by D.H. Janzen and W. Hallwachs from 1978 to 1984 (this replaces the checklist for Santa Rosa in Haber 1983).

2/ Species that breed in Santa Rosa each rainy season, as based on finding larvae or large numbers of both sexes of adults and females with variously expended egg loads.

3/ Based on the thorough distribution records reported in Schreiber (1978), and amplified by J.M. Cadiou. Also supplemented by D.H. Janzen and W. Hallwach's survey of moths of Costa Rica (ongoing) and collection records of W.A. Haber, F.G. Stiles and I. Chacón in Costa Rica. "Caribbean" refers to islands other than Trinidad, which is in part just an amputated Venezuelan peninsula, from an ecological viewpoint.

4/ "R" = apparently breeds in Costa Rican lowland rainforest, as based on widespread collection in this habitat. "D" = apparently breeds in Costa Rican lowland dry forest, as based on widespread collection (and usually, finding caterpillars) in this habitat. "R(?)" refers to species that are common in dry forest but occasionally occur as adults in marginal rainforest habitats such as Monteverde (Haber 1983) that may be simply moist areas in which to pass the nearby severe dry season or may be breeding sites. "D(?)" refers to species that are probably dry forest breeding species but are so rarely collected in Costa Rica that their breeding site cannot be known with any certainty.

5/ This pair of *Perigonia* were treated by Schreiber (1978) as two species, which they clearly are at Santa Rosa; however, many collections and sphingid collectors traditionally treat them as two subspecies of *Perigonia lusca*. In Janzen (1985b, 1984b) they were treated as one species, *Perigonia lusca*. This matter will be treated in greater detail in a forthcoming publication.

6/ Species that are encountered at very rarely Santa Rosa, but since occasional caterpillars are found and both sexes are taken at flowers and lights, I suspect them to be rainforest or cosmopolitan species that only occasionally make use of Santa Rosa for breeding.

7/ Species that clearly maintain breeding populations in other parts of Costa Rica and are encountered at Santa Rosa only as single individuals at several year intervals; such species are often termed "strays" by sphingid biologists.

Table 3. Size of *Perigonia ilus* (Sphingidae) taken at lights in Santa Rosa National Park (April-July 1984). All specimens are males in good condition, and all individuals that arrived at the lights were included.

	Dry weight of entire moth (g)		Length of forewing (mm)	
Date of capture	$\overline{X}$	s.d.	$\overline{X}$	s.d.
April-May, arriving males, n = 37	29.6	1.5	0.327	0.072
June-July, first Santa Rosa generation, n = 8	26.9	2.7[1]	0.213	0.057[2]

1/ Weights significantly different, $p < .05$, $t_{43\,\mathrm{d.f.}} = 2.77$

2/ Wing lengths significantly different, $p < .01$, $t_{43\,\mathrm{d.f.}} = 5.10$

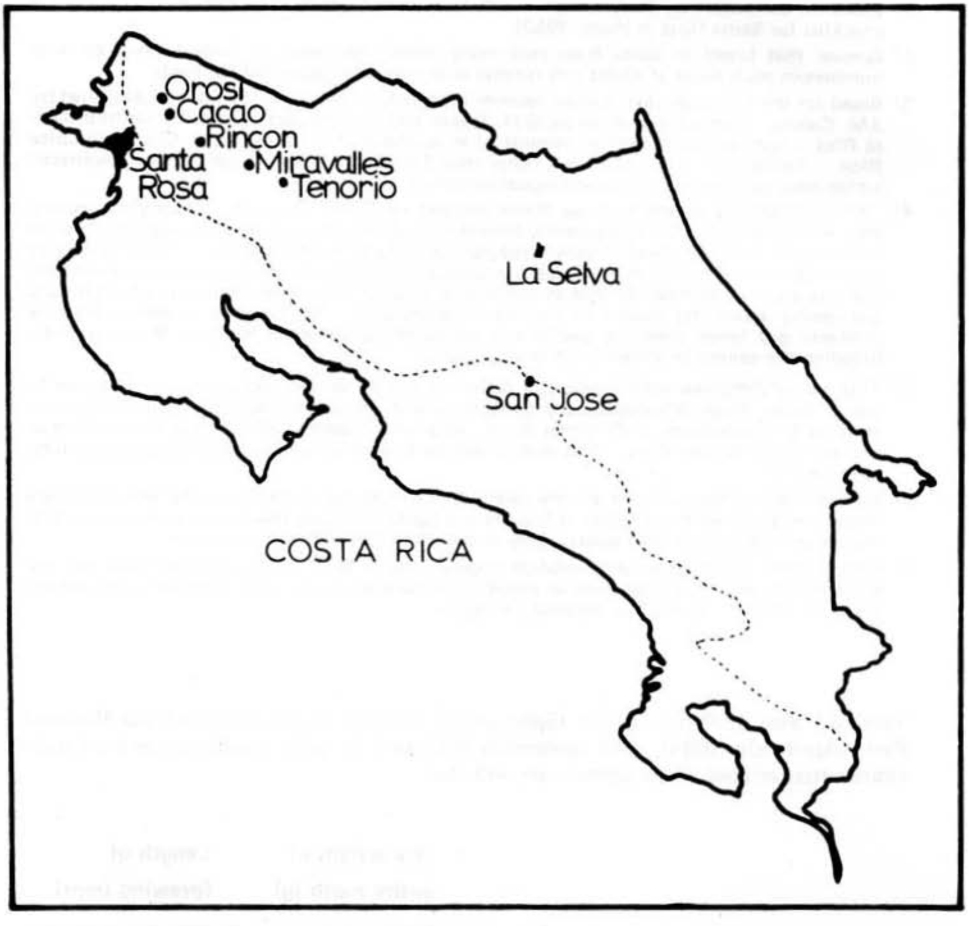

Figure 1. Location of Santa Rosa National Park in northwestern Costa Rica. The Cordillera de Guanacaste is indicated by the five volcanic peaks to the east of the Park. The Cordillera separates the dry forest lowlands of the Santa Rosa area from the rainforested lowlands of northern and northeastern Costa Rica. La Selva, the field station of the Organization of Tropical Studies, lies on the southern margin of these lowlands, which continue northward through eastern Nicaragua. The dotted line is the Interamerican Highway.

Figure 2. Seasonal change in Santa Rosa forest. A. Interior of 60-80-year-old secondary successional forest in July. B. Same photograph as A but in March.

A

B

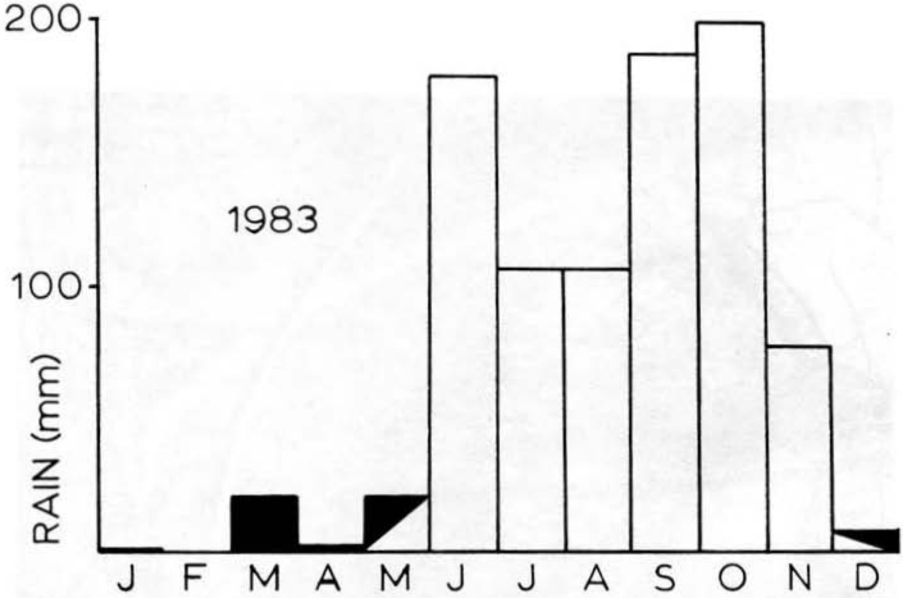

Figure 3. Monthly rainfall for a representative low rainfall year at Santa Rosa National Park (Administration Area). The dark areas indicate what is generally the long dry season. The 22.7 mm of rain in March fell in a two day period. Most of the July-August rain occurred near the beginning and end of this seasonal low.

Figure 4. Adult of the species of *Enicospilus* (Ichneumonidae) that is a monophagous parasitoid of *Rothschildia lebeau* (Saturniidae) in Santa Rosa National Park. Wasp is 2 cm long. August 1984.

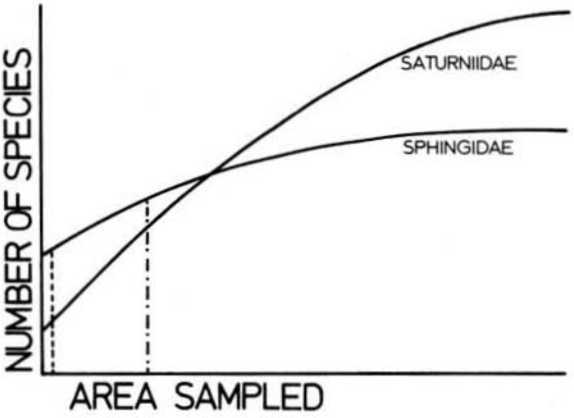

Figure 5. Hypothetical representation of the species-area curves for Saturniidae and Sphingidae summed over large Neotropical areas. The dashed line represents an area like Santa Rosa National Park while the dot-dash line represents an area like Costa Rica.