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Natural History of *Hylesia lineata* (Saturniidae: Hemileucinae) in Santa Rosa National Park, Costa Rica

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ABSTRACT: *Hylesia lineata,* a hemileucine saturniid of the Pacific side of Central America, is exceptional among the 30 species of saturniids of the deciduous forests of Santa Rosa National Park, Costa Rica (0–350 m elevation). It passes the dry season in the egg stage, lays all its eggs in one egg nest, and has strongly urticating hairs on the adult (female only). In addition, this small moth exhibits enormous fluctuations in adult density among years, has caterpillars that feed on at least 46 species of plants in 17 families (but females prefer a smaller number of species for oviposition sites), grows very slowly as a caterpillar, is polymorphic in color as both caterpillar and adult, and has longer male than female pupal duration (resulting in synchronous emergence of the sexes).

In the lowland deciduous forests of northwestern Guanacaste Province, Costa Rica, and specifically in Santa Rosa National Park, the small hemileucine saturniid *Hylesia lineata* Druce (Fig. 1) is of conspicuous ecological interest for two reasons; its population in Santa Rosa fluctuates enormously in density among years, and it is the only one of the 30 resident species of saturniids (Janzen, 1982a) that passes the dry season as eggs rather than as pupae (*Hylesia dalina* Schaus may also do so, but its immature stages are unknown). As part of a long-term ecological study of the moths of Santa Rosa National Park, I here describe the details of the natural history of *H. lineata* in hopes that it will encourage others to examine the much neglected and drab members of the huge neotropical genus *Hylesia* (at least 200 species, C. Lemaire, pers. comm.), and to have these details available for comparison with those of the other saturniids at Santa Rosa. *Hylesia* larvae and adults have been of note to date largely as urticating insects (e.g., Marsh and Pinango, 1971; Pesce and Delgado, 1971; Lamy et al., 1982; Lamy and Lemaire, 1983), and *Hylesia* is well-known to saturniid biologists as badly needing systematic revision (R. Peigler, C. Lemaire, pers. comm.) despite the existence of several taxonomic treatments (e.g., Packard, 1914; Draudt, 1929; Druce, 1881; Dyar, 1913).

The Study Site

Santa Rosa National Park is 25 km south of the town of La Cruz, between the Pan-American Highway (Costa Rica Highway 1) and the Pacific Ocean. Its 10,800 ha rectangle encompasses a plateau (200–350 m elevation), the steep southwest-facing escarpment, and the adjacent small coastal plain. The vegetation is primarily deciduous forest but contains small patches and thin lines of evergreen forest associated with seasonal watercourses or high water tables. Large portions of the Park were an operating cattle ranch from about 1700 until about 20 years ago, and the pastures are gradually returning to woody vegetation. There are about

Fig. 1. Adult *Hylesia lineata*. Upper left: pink morph, gravid female. Center: gray morph, gravid female. Lower right: gray morph, female after oviposition. Remaining individuals with normal male coloration, except top center specimen has unusual yellow centers to eye-spots on hind wings (Santa Rosa National Park, Costa Rica).

650 species of broadleafed plants in the Park (Janzen and Liesner, 1980). Various descriptions of Santa Rosa can be found in Boza and Mendoza (1981), Bonoff and Janzen (1980), Janzen (1981, 1982a, 1982b), Fleming and Heithaus (1981), and Fleming (1981). Between 1500–2000 mm of rainfall between early May and early December (unpublished weather station records), and the rain-free 5–6 month dry season is windy and sunny; after the first 1–2 months of the dry season, herbaceous vegetation is sufficiently dry to burn freely, many of the deciduous tree species are leafless, forest litter and soil surfaces are extremely dry, and even at night the relative humidity may be as low as 80–90%. The Santa Rosa vegetation was once part of a lowland belt of deciduous forest from about Panama City, Panama, to Mazatlan, Mexico, with evergreen forest interruptions in southwestern Costa Rica and in the area of northwestern Guatemala to Chiapas, Mexico; however, at present, at least 95% of this vegetation type has been totally cleared for crop lands or pastures, or severely degraded by lumbering and cattle. This vegetation type also extended across the Isthmus of Tehuantepec, Mexico, and thence northwest to the Tropic of Cancer on the coastal plain of Mexico and northeast into the Yucatan Peninsula.

Geographic Distribution of *Hylesia lineata*

Hylesia lineata was described from Costa Rican specimens take at 2000 m elevation on Volcan Irazu (Druce, 1881:197) in the central highlands of Costa Rica. Conte (1906) described it as "*Automeris ondulatus*" from San Jose, Costa Rica; Draudt (1929) synonymized *H. ondulatus* (Conte) with *H. lineata* and I agree with this placement. I have collected *H. lineata* adults in habitats ranging from lower montane rainforest (e.g., Park Headquarters, Rincon National Park, Guanacaste Province, 700 m elevation) to the driest lowlands of Guanacaste Province. However, all collection records are from the Pacific side of Costa Rica, except for Volcan Irazu, which may be viewed as central. One male was taken at light at Las Alturas, Puntarenas Province near the border with Panama (1600 m; P. J. DeVries, collector) and I collected one male at nearby Finca Las Cruces, near San Vito de Java (1200 m). It occurs as far north as Estacion Biologia Chamela, 70 miles north of Manzanillo, Colima, Mexico (100 m elevation; personal collection of a newly emerged male, and Alfonso Pescador, pers. comm.) and as far south as Panama (C. Lemaire, pers. comm.). Draudt (1929) records its distribution as Mexico to Panama. I suspect that *H. lineata* has a distribution encompassing the entire Pacific coastal plain of Central America and tropical Mexico, with various incursions into the more central upper elevations. However, determining its geographical distribution will always be difficult because it may be extremely rare for several successive years at a site where there is a breeding population (see below).

Adult Moth

COLOR, APPEARANCE, AND BEHAVIOR: *H. lineata* (Fig. 1) is the most distinctive of the Costa Rican *Hylesia* (so much so that Druce (1881:197) was not even comfortable in placing it in *Hylesia*), and is unlikely to be confused with congenerics in other parts of the Neotropics. The sexes are quite different from each other in wing shape, size, color and degree of color variation. Field-caught males weigh 0.05–0.11 g and females 0.12–0.35 g (live weight).

I have bred the two color morphs of the females from a single clutch of eggs on numerous occasions; the females are either generally brown with slightly gray overtones, or the same color with a light pink wash over all colors (Fig. 1). When the female is at rest on foliage, she is very cryptic. Her forewings are held so as to form a low tent over the back, with the posterior margins slightly overlapping; in this position the body colors are not visible and the female looks very much like a dead dry leaf with a slightly undulating or crinkled surface. The scales on the forewings are somewhat sparser than normal for saturniids, giving the wings a slightly shiny appearance, even if the female's wings are not worn or tattered.

When disturbed by prodding or a sudden movement in her vicinity, the female abruptly raises her wings high over her dorsum and holds the dorsal surfaces together; the large abdomen is then strongly curled under, making a large furry display of dark and light orange rings (Fig. 2). While displaying, the female holds tightly to the substrate; if she is pushed, she will release her hold and drop to the litter, but she keeps the motionless wings held high and together, with the abdomen curled under. In this position and behavior, she closely resembles specimens of *Dirphia avia* (Stoll.) and *Periphoba arcaei* (Druce) in their defensive postures;

Fig. 2. Living female *H. lineata* in defensive posture, with abdomen strongly curled and wings held together and rigidly over the dorsum; in front of her is a new felt-covered egg nest made by a different female *H. lineata*.

these two hemileucine saturniid moths are common in Santa Rosa and are rejected by ants and vertebrate predators, possibly because of their strong odor (unpubl. observations).

When molested, female *H. lineata* display no behavior that could be interpreted as an attempt to throw or push the abdominal hairs at the attacker (see later discussion of why this might be expected). Once the annoyance has stopped, she returns her wings to the previous tent-like position over her dorsal side. I have never seen a *H. lineata* female (mated or unmated) attempt flight when attacked by me or a mouse (day or night). However, if attacked by a mouse (see below), she will drag herself away with her legs. Fully gravid female *H. lineata* can fly, however, as I have seen them fly to lights at night and flying in the forest at night in the beam of a flashlight. Neither sex flies during daylight hours if undisturbed.

The males occur in at least five color morphs and a variety of intergrades, ranging from almost yellow to nearly maroon-black; the most common are pink-

Fig. 3.   Living male *H. lineata* in normal resting posture.

ish, olive-drab, beige-brown, rust or gray (Fig. 1). I have reared males of all different colors from eggs of a single female. All colors do not occur with equal frequency; yellow, orange, bright rust and deep maroon are the rarest colors (about 15% of the total in a brood) and the more somber colors are the most common. At rest, the males hold the wings in a shallow tent over the back such that they completely conceal the abdomen and hind wings (Fig. 3), except that sometimes the anterior margins of the hind wings project 1–2 mm forward of the anterior margins of the forewings. The wings are densely scaled (not slightly shiny as in the females) and the dense velvety surface looks like a flat, dry, and slightly tomentose leaf crossed by several dark lines. As is the case with females, the males perch on the vegetation in the daytime, and may be found on virtually any kind of background.

When molested, the male spreads his wings in a nearly horizontal plane, displaying the hind wings, just as do both sexes of the hemileucine saturniid genus *Automeris*. The center of each *H. lineata* male hindwing has a slightly blurry but conspicuous "eye spot", with a red (usually) or yellow (rarely) center surrounded by a black ring (Fig. 1). The male abdomen is small and lightly ringed in dark on the ground color of the wings; it is only gently curled and not very conspicuous during the defense display, and does not appear to play a major defensive role. Male *H. lineata* do not attempt to fly when gently disturbed. If attacked viciously, the male either drops to the ground and further displays the eye spots, or launches into rapid flight; at the daytime warm temperatures prevalent at Santa Rosa, little or no "warm-up" time seems to be necessary for flight. If a male *H. lineata* flies, he usually moves tens of meters or more before again coming to rest and hiding the hindwings beneath the forewings. Upon alighting, the body and wings are

rocked from side to side several times as though "settling" into place. Such movement by *Automeris,* a genus closely related to *Hylesia,* has been viewed as being of totally unknown adaptive significance (Bastock and Blest, 1958). However, the behavior appears to be of direct adaptive value because it makes the motion of the moth coming to rest after flight appear more like the movement of a leaf blown by a slight breeze.

ECDYSIS AND PRE-MATING BEHAVIOR: Adult *H. lineata* emerge from the cocoon in mid-afternoon in nature, at about the time when the light intensity in the forest understory is distinctly diminishing. If kept indoors, the adults sometimes emerge from their cocoons as early as 1300–1400 hours if the room is poorly illuminated through shaded windows.

Newly emerged adults climb up the side of the container and stop after walking only 10–20 cm. The wings first expand in the usual pendant position, and then are moved into the plane of the substrate and thence to the usual resting position. The moth displays no wing shaking (as occurs in the much larger saturniids, *Caio championi* (Druce) and *Titaea tamerlan* (Maassen), at Santa Rosa) or other unusual behavior associated with wing expansion. In the field, newly emerged adults climb 20–100 cm up vegetation from the cocoon site before settling and expanding the wings. In both sexes, about 5 hours are required for the wings to become fully hardened (however, the wings of females remain much more flimsy and supple than those of the males). A female *H. lineata* begins to pheromonally call males 3–4 hours before dawn of the same night that she emerges from the cocoon, and she continues to call until sunrise if not mated. Males first appear at lights hung in the forest around midnight and continue to arrive until the sky is pale gray with dawn; there is often a very distinct peak in numbers to arrive at about the moment of the first light of dawn. This flight period is in striking contrast to that of *Hylesia dalina,* the only congener of *H. lineata* in Santa Rosa; *H. dalina* males arrive at the light almost entirely before 2200 hours (about 4 hours after the onset of dark). Females of *H. lineata* arrive at lights at all hours of the night, while those of *H. dalina* almost always arrive before 2200 hours.

Copulation attempts have not been observed, but copulating pairs were commonly encountered at dawn hanging of the foliage during the 1979 peak emergence (see below). They remain together all day unless disturbed. During the morning, a pair of *H. lineata* requires rather severe disturbance to separate; in the afternoon they separate with only gentle prodding. When a newly emerged moth is disturbed, in addition to performing the display described earlier, it also readily and forcibly ejects meconial fluid from the anus. This fluid is mildly disagreeable in odor, but no more so than the meconial fluid of other species of Santa Rosa Saturniidae.

A newly emerged male will launch into flight if strongly disturbed any time after about 5 hours after emergence. If newly emerged males are placed on foliage on the evening of the afternoon of their emergence, they leave the site by midnight or shortly thereafter. Unmated females do not attempt to fly on the first or second nights of adult life, but may change positions in a large cage by walking or walking accompanied by very rapid fluttering of the wings; in nature this might result in flight, but since other saturniid females actually fly in the cages in the same situation, I suspect that it does not.

Unmated female *H. lineata* live 4–6 nights before dying ($n = 12$); during this time they do not lay their sterile eggs. This is in striking contrast to many other

Fig. 4.   Female *H. lineata* hanging on a hair rope below her felt-covered egg nest produced a few hours before.

species of Santa Rosa saturniids that have been prevented from mating. Unmated males live 3–6 nights ($n = 20$). Both longevity records listed above are based on reared adults kept in screen cages (females) or large plastic bags at room temperature (males); these particular adults were about 10% lighter (live weight) than the adults emerging from cocoons collected in the wild. As is the case with other hemileucine saturniids, the adults lack functional mouth parts and show no behavior that could be interpreted as an attempt to feed.

Eggs

OVIPOSITION BEHAVIOR: Once a female *H. lineata* has selected an oviposition site, she hangs from the twig or leaf petiole and curls her abdomen up to the substrate; she lays all her eggs at once while simultaneously twisting her abdomen around the twig and egg mass such that the long loose abdominal hairs form a dense felt covering around the egg mass (Figs. 2, 4, 5). The densely packed and apparently defensive short hairs (see below) are pulled free from the body among the long hairs, and are therefore tightly packed into the felt layer around the eggs. The outer portion of the felt is mostly long hairs and the inner portion of the felt mostly the short hairs. Each of the long hairs bears many lateral distally-pointed barbs (Fig. 9c) on its proximal half. The barbs catch on other hairs as they are drawn away from the body, and thereby stick tightly together. The long projections at the proximal end probably serve to twist the hairs as they pass between other

Fig. 5. Felt-covered egg nest of *H. lineata*, torn open to expose the eggs.

hairs. The short urticating hairs (Fig. 9b) are interspersed with the long hairs and drawn out with them. No glue-like material appears to be involved in construction of the felt outer layer of the egg nest, though the eggs are lightly glued to each other and to the layer of hair between them and the stem. As construction of the egg nest nears completion, the female often releases her hold on the substrate and suspended from a thin short rope of her own hairs, she twists in the air below the egg mass (Fig. 4); this appears to tighten the packing of the felt around the egg mass. On occasion the rope is too strong for her to eventually break free, and the next morning she remains suspended in a moribund state beneath her egg nest (Fig. 4).

It appears that all eggs (Fig. 5) are deposited in a single oviposition event. I have collected a total of 63 wild females from which the abdominal hairs have been removed (at light, sitting on foliage) and only 4 contained more than 1 egg; these 4 contained 3, 3, 6 and 7 eggs. I have watched 6 ovipositions in the field and 12 in plastic bags in the laboratory, and in all cases, all eggs were laid at one time in one egg nest. Wild-caught females with abdominal hairs intact and females
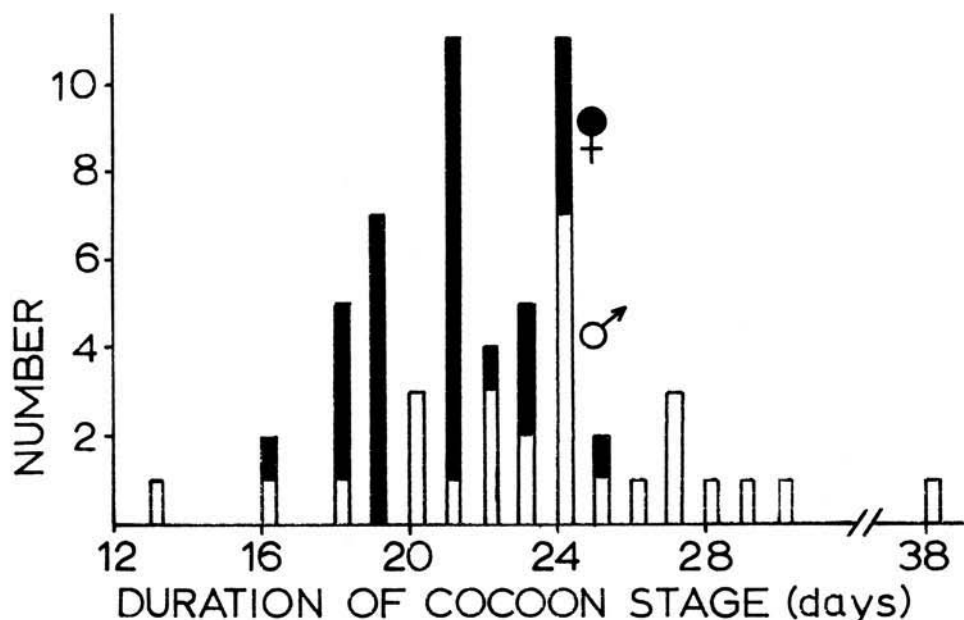
Fig. 6.   Duration of cocoon stage at forest temperatures for 59 *Hylesia lineata* reared on a variety of host plants in the first half of the rainy season, 1979.

that emerged from cocoons collected in the wild ($n = 25$) contained a mean of 298 eggs (SD = 95.7) (range: 101 to 450) and 30 egg masses collected in the same area as were these females, contained a mean of 302 eggs (SD = 94.3) (range: 113 to 434): these are not significantly different means.

The egg nest of *H. lineata* is similar to that described for two other species of *Hylesia*. Crotch (1956) noted that "the female of *H. nigricans* lays her eggs in layers on a plane surface (the wooden supports of a cage), covers them with urticating straw colored hairs from the sides of her abdomen, repeats the process with a smaller layer, until perhaps a hundred are converted into a tiny cocoon-like bundle". Winder (1976) said that the eggs of *Hylesia* prob. *fulviventris* are "laid in compact, hemispherical masses on the secondary branches of *Lantana tiliaefolia* from January to April in the Curitiba region, and are completely covered with a light brown, fibrous coat."

If the female *H. lineata* lays her eggs the first night after mating (second night as an adult), she does not die that night ($n = 6$); if she lays her egg mass on the third night as an adult ($n = 4$), she is dead by morning. About 12% of the females that arrive at lights have already laid their eggs, and I suspect that these are among the females that oviposited in the first night after mating. It seems likely that the mated female has about 4 nights of flight in which to find an oviposition site, and she then dies irrespective of which night was the oviposition night. Since she is genetically dead once she has laid her eggs, there is no way to directly select for her death immediately after oviposition on the first night, *if* she is to have the capacity for 4 nights of search for an oviposition site. In fact, she may even continue to search for oviposition sites once she has laid all her eggs.

An egg nest of *H. lineata* looks like a large smooth spider egg case (Figs. 2, 4), is dark beige in color initially (but dries and fades to light beige in the dry season), and is soft but firm to the touch. The felt layer is very tough and requires considerable effort to rip apart. If the branch bearing an egg nest is very actively shaken by the wind, the attachment site of the egg nest may eventually come loose, but the egg nest does not fall off since the felt encircles the stem. Egg nests from which the larvae or ovarian parasites have emerged remain on the stems for many months; in July 1980 there were still many old egg nests on living twigs that dated from the heavy oviposition in late July 1979.

OVIPOSITION SITES: I have conducted no experiments on choice of oviposition site by *H. lineata,* but as the egg masses are conspicuous and easy to find in the vegetation, some inference about choice of sites is possible.

The Santa Rosa vegetation is a highly heterogeneous mix of herbaceous vegetation (old pastures, roadsides) and woody vegetation of all ages and sizes. While newly laid *H. lineata* egg nests were encountered throughout these vegetation types, they were conspicuously absent from herbaceous vegetation. In herb-rich habitats, the egg nests were found on the woody branches of low shrubs (e.g., *Cassia biflora*) and isolated shrubby trees 2–5 m in height (e.g., *Guazuma ulmifolia* and *Gliricidia sepium*); I collected or tallied well over 500 egg nests in 1979 and only one was on a herbaceous plant—*Sesbania emerus,* a 3–4 m tall very stiff herbaceous analogue of a small tree.

Most egg nests are constructed on woody twigs 1–4 mm in diameter. If egg nests are collected in the dry season, all those encountered are on such substrates. However, in July–August 1979 (mid-rainy season), many egg nests were also found on the 2–4 mm diameter petioles of large leaves of the same woody plants whose twigs were also used as oviposition sites. There are two possible ways that this pattern could have been generated. It may be that the females do not discriminate between petioles and twigs in the mid-rainy season (and need not do so since the leaf is unlikely to be shed in the 2 week period before the larvae emerge) and the second generation females oviposit in November–December only on woody structures unlikely to be shed during the upcoming dry season. Of 122 egg nests recorded in December 1979, none were on leaf petioles. On the other hand, it may be that the second generation females are just as indiscriminate as are the first generation females, and the falling leaves move part of the egg nests to the litter where I did not notice them. However, I suspect that this is not the case since the females do not place the egg nests close to or in the litter, which implies that the litter is a dangerous area for the female or the egg nest.

Virtually all egg nests are placed between 30 and 250 cm above the ground, with most being 40–150 cm above the ground. There is one conspicuous exception; when a shrubby tree (e.g., *Guazuma ulmifolia, Lonchocarpus minimiflorus, Gliricidia sepium*) is growing alone in a pasture or fencerow, egg nests may be placed as high as 4 m above the ground if there are no lower branches.

The egg nests are not homogeneously distributed through the vegetation in forested habitats. Many more are found on branches along edges (e.g., banks of large streams, roadsides, margins of old burned areas and tree falls) than in heavily shaded forest understory. I suspect that this distribution is due to such sites having both higher quality food and a high density of favored species of food plants. For example, at Santa Rosa the foliage of *Casearia corymbosa* appears to be high

quality food for *H. lineata*. *Casearia corymbosa* shrubs and treelets occur through-out the 20–80 year old second growth forests in the vicinity of the administration area, but the *C. corymbosa* on edges received many more egg nests than did those in the forest understory. A *C. corymbosa* growing in intermittent isolation gen-erally bears 5–20 times as many leaves as does one of the same age growing in heavily shaded understory a few meters away.

The apparent preference for sunny places for egg nests expressed itself in a very specific manner. Egg nests could be found most quickly by locating a *Casearia corymbosa* crown at the edge of a tree fall or on a creek bank, and then searching whichever branch projects farthest from the crown into the opening. If there were many egg nests in a partly shaded crown, then there would be more on the branches that projected into the clearing than on the shaded branches. Such oviposition sites were chosen by the moth after dark but it could use exposure to starlight or moonlight as an indicator of the eventual exposure to sunlight.

While *H. lineata* caterpillars feed on the leaves of a wide variety of species of woody plants in nature, the egg nests are not placed randomly with respect to species of plants and the caterpillars are not found eating all species of plants. I have never found a larva of *H. lineata* feeding on a herbaceous plant (viny or self-supporting) but observed tens of thousands of *H. lineata* caterpillars in 1979. Second, the caterpillars in nature are certainly not distributed uniformly or ran-domly over the species that are fed on. At Santa Rosa during the 1979 peak density of *H. lineata,* most plants of *Casearia corymbosa* (Flacourtiaceae), *Ca-lycophyllum candidissium* (Rubiaceae), and *Guazuma ulmifolia* (Sterculiaceae) had some caterpillars and many were defoliated. In the same habitat at the same time, the following species commonly had some caterpillars of *H. lineata* but were never defoliated: *Muntingia calabura* (Elaeocarpaceae), *Casearia sylvestris* and *Zuelania guidonia* (Flacourtiaceae), *Acacia tenuifolia, Bauhinia ungulata, Diphysa robinioides, Enterolobium cyclocarpum, Hymenaea courbaril* and *Lon-chocarpus minimiflorus* (incorrectly called *L. nitidus* in Janzen, 1981) (Legumi-nosae), *Guettarda macrosperma* (Rubiaceae), *Allophyllus occidentalis* and *Urvillea ulmacea* (Sapindaceae), *Leuhea speciosa* (Tiliaceae). Finally, there was a set of species on which only very rarely were caterpillars encountered feeding: *Tabebuia rosea* (Bignoniaceae), *Bombacopsis quinatum* (Bombacaceae), *Cordia alliodora* (Boraginaceae), *Hirtella racemosa* (Chrysobalanaceae), *Casearia arguta* (Flacour-tiaceae), *Persea americana* (introduced) (Lauraceae), *Cassia biflora, Dalbergia retusa, Gliricidia sepium, Inga vera, Lonchocarpus costaricensis, Lysiloma auri-tum, Machaerium kegelii, Mimosa pigra, Myrospermum frutescens* and *Pithecel-lobium lanceolatum* (Leguminosae), *Hyptis pectinata* (Labiateae), *Malvaviscus arboreus* (Malvaceae), *Banisteriopsis muricata, Byrsonima crassifolia,* and *Stig-maphyllon ellipticum* (Malpigiaceae), *Erythroxylon havanense* (Erythroxylaceae), *Cupania guatemalensis, Paullinia cururu* and *Serjania schiedeana* (Sapindaceae), *Byttneria aculeata, Byttneria catalpaefolia* and *Triumfetta lappula* (Sterculiaceae), *Lantana camara* (Verbenaceae). All 46 species of plants listed above (17 families) are common plants, and plants in each category grow side by side with plants in the other categories.

The distribution of caterpillars in nature is a product both of where oviposition occurred and how the caterpillars behave. While I did not keep detailed numerical records on the location of egg nests, their relative abundance on woody plant parts

agreed quite well with the three above categories. At the extreme, at least a third of the egg nests were on *Casearia corymbosa* twigs, and a 2 m shrub on the edge of a clearing might have as many as 30 egg nests placed on it in the July 1979 peak of oviposition. I was left with the impression that a female *H. lineata* searched for a *C. corymbosa, G. ulmifolia* or *C. candidissimum* and if one was not found, there were a larger number of other species that were acceptable oviposition sites. I should emphasize that there were at least 200 species of woody plants growing adjacent to those listed above and on which egg nests or caterpillars of *H. lineata* were never found. *Hylesia lineata* did not use at least 85% of the species of broad-leaved plants in the habitat for oviposition or larval hosts.

There was also a hint that females chose oviposition sites for traits other than the species of plant and its location in the habitat. When a number of similar-appearing individuals of the same larval host species were growing in the same site, it was commonplace for each to receive quite different numbers of egg nests. The most extreme case was offered by a row of 24 *Gliricidia sepium* living fence-post trees along the edge of an abandoned pasture. The trees were spaced at 4–5 m intervals and 3–4 m tall; 23 trees received no egg nests and one received 17. This tree was number 9 counting from one end of the row, and did not differ from the other trees in any conspicuous manner. This row of trees presumably originated in the usual asexual manner; living branches were cut off of other fencerow trees (or occasionally, other wild trees), and planted in the ground to grow into new trees. I suspect that the acceptable *G. sepium* had a different genetic origin from that of the 23 rejected trees.

Caterpillar behavior (see below) may distribute the larvae among hosts in a slightly different manner than does oviposition. However, since the larvae do not generally leave the plant on which the egg nest was laid (unless they consume all the leaves or are attacked by a vertebrate), the distribution of larvae observed in nature is about the same as that of the distribution of egg nests (see below).

Larvae

If the egg nest is made during the middle of the rainy season, the larvae emerge from the eggs and nest about 2 weeks after the eggs are laid. If the egg nest is made at the end of the rainy season (November–December), the eggs remain dormant and hatch about 2 weeks after the first soaking rains in early May. In either case, the newly emerged larvae remain together in a compact group for the first 3–4 instars. During the day, during the first 2–3 instars, they rest side by side in a monolayer patch on the trunk or a large stem of the host plant. In these stages, they are light brown in color, and bear a dense covering of whitish branched urticating spines. As many as 300 larvae may be in one such patch. I do not know if several clutches will coalesce into larger groups, but I doubt it, since groups larger than about 300 larvae are not encountered. At dusk, the larvae march off in a very long procession, head to tail, to the crown of the host plant and feed as a large group on the old leaves of a particular branch (see Capinera, 1980, for a discussion of this trail-forming behavior by another hemileucine saturniid). They normally eat only the mature leaves; the shoot tips, expanding leaves and light green leaves are left uneaten. The selective feeding behavior is especially con-spicuous when feeding on legumes. By dawn they reappear as a patch on the tree trunk, sometimes at the same place as in the previous day.

Fig. 7. Fourth instar *H. lineata* caterpillars from one egg mass. The light-colored caterpillar is predominantly light green.

After molting to the fourth instar, the larvae no longer rest on the tree trunk, but instead bind numerous leaves together with silk into a hollow irregular mass. During daylight hours they remain inside, where they are adjacent and sometimes one on top of another. Each nest contains 10–50 larvae, and several such nests are usually produced by the larvae from one egg clutch. The larvae may return to such a nest for several consecutive days, but then they usually abandon it for another one constructed on a nearby branch. It is widely known that the caterpillars of *Hylesia* gregariously build silk and leaf nests, and leave them at night to feed (e.g., Draudt, 1929:749–750), but there has been no detailed study of this behavior.

In the fifth and sixth instars, the group of caterpillars breaks up and individuals pull several green leaves together to form a diurnal resting chamber; as many as five caterpillars may be encountered in one such chamber, but the larger the caterpillars, the more likely there is to be only one per chamber. In the fifth and sixth instars, the larvae occur in two color morphs (Fig. 7). One morph is light green with a dark green dorsal stripe and nearly white fine longitudinal lines on the back and sides. The long and branched urticating spines are pale green. The other morph is dark greenish-black, with nearly white and thin longitudinal lines and dark gray green urticating spines. Both color morphs have black and white head capsules, but there is more black on the head capsule of the dark morph. After several years of preservation in alcohol, the caterpillar color morphs can still be distinguished.

In no case do the larvae feed on the leaves in the nests unless all the other leaves on the tree have been consumed. Additionally, the larger (older) larvae seem less inclined to avoid eating young leaves; when a tree is fully defoliated, leaves of all ages are eaten.

While a large *H. lineata* caterpillar is occasionally encountered feeding or resting

as much as 4–5 m above the ground, the vast majority of the caterpillars are in leafy foliage 0.5–2 m above the ground. However, if the leafy part of the vegetation is uniformly tall (e.g., 5–8 m), such as the case where an old pasture is returning to woody vegetation through even-aged regeneration of *Lonchocarpus minimiflorus,* the caterpillars of *H. lineata* are usually found at the height of the plant crowns.

If there is adequate foliage for larval development on the crown of the plant on which the egg nest was placed, the larvae pass all their growth stages on the plant. However, if the plant is defoliated, the caterpillars wander off, presumably in search of more food. They do not feed on just any species of plant that they encounter; however, if they encounter any one of the species on which egg nests are also found, they continue to feed. The survivorship and weight of larvae forced to change species of host plant after partial development is not known, but preliminary experiments with caterpillars in 1979 suggested that in some cases the larvae could change hosts and continue to develop and in others, they could not do so. Caterpillars that were moved from *Lonchocarpus minimiflorus* leaves to *Casearia corymbosa* leaves, and vice versa, increased in weight conspicuously more slowly than did caterpillars allowed to remain on diets of the plant species on which their egg nests had been placed. There is a second opportunity for individual larvae of *H. lineata* to change hosts. When the caterpillars are physically disturbed (especially when the diurnal resting nest is torn open), they release their hold on the substrate, thrash about, and fall off the plant. The caterpillar does not spin a silk guideline when it falls. It must find its way back to a host plant by haphazard search. Searching caterpillars climb whatever vertical substrate they encounter and then move laterally through the vegetation (from branch to branch) once they have reached a height of 1–2 m above the ground. I do not know what fraction regain the original host or a plant conspecific with it, but there is the opportunity for changes of host.

I do not have detailed records on *H. lineata* growth rates, but in 1979, masses of newly emerged first instar larvae were common during the first week of May (first heavy rains were in late April) and cocoon-spinning pre-pupal larvae were abundant on the same vegetation at the end of June. Well-fed larvae weigh 2.2 to 3.5 g just before cessation of feeding. Approximately 7–8 weeks appears to be the usual developmental time for free-living *H. lineata* caterpillars.

On occasion, *H. lineata* larvae are found feeding on the leaves of plants on which they later die of apparent starvation (e.g., *Crescentia alata* and *Acrocomia vinifera*). I suspect that these are larvae that became lost from their original host plants and were feeding as a test of the suitability of the plants they had found.

Pupation

Upon cessation of feeding, the larva defecates its gut contents; as is usual in Lepidoptera, this final fecal matter is more moist and less well formed into pellets than are normal feces. In contrast to the larvae of many other Santa Rosa saturniids, the pre-pupal stage of the last larval instar does not change color. It walks off the host plant for a distance of 1–5 m over litter and arboreal pathways, and then settles among green living leaves 20 to 150 cm above the ground to spin a cocoon. On edges on woody vegetation, the wandering often takes the caterpillar into purely herbaceous vegetation where it cocoons among herbaceous foliage of species

that are never eaten by *H. lineata*. On the other hand, its wandering may also take it into the foliage of a plant conspecific with its host plant, and it may cocoon there as well. The outcome is that cocoons may be found among the arboreal leaves of virtually any species of plant in the habitat (as well as on foreign objects such as between strips of plastic flagging). Even in areas of very high cocoon density, I was able to find no cocoons among litter on the ground despite intensive search. "High cocoon density" is, for example, finding 216 living cocoons during a one hour search of an area of 10 × 20 m of herbaceous vegetation (Compositae: *Melampodium divaricatum*) adjacent to woody second growth rich in *Loncho-carpus, Casearia* and other plants edible to *H. lineata* (30 June 1979). There is no suggestion of communal pupation.

The cocoon is made by pulling together two leaves or folding one over such that most of the cocoon wall is spun against the leaf, but some of it self-supporting. The silk is medium-brown in color, with most variation in the direction of being lighter in color rather than darker. The silk wall is very tough. Although thin, it is opaque and stiff. When larvae are being reared in plastic bags, they readily spin cocoons among the folds of plastic. Inside the cocoon, the pupa is firmly fixed to the silk at its posterior end by a cremaster bearing recurved hooks. Pupation occurs about 48 hours after spinning begins. The pupa is dark brown in color.

I have reared over 500 *H. lineata* to the adult stage from larvae or pupae collected in the field at Santa Rosa, and in no case did the pupa enter into a period of extended dormancy (38 days was the maximum duration of the period from spinning to emergence of the adult). This behavior sets *H. lineata* apart from all of the other 14 saturniids that I have reared at Santa Rosa, in that it does not become dormant even when the cocoon is in a very dry plastic bag (however, I have not reared *Hylesia dalina*). This lack of pupal dormancy is in agreement with the observed behavior of adults in the field. No *H. lineata* have been taken at lights before the end of the second month of the rainy season, even in the year of peak abundance (1979); it therefore seems very unlikely that *H. lineata* ever passes the six-month dry season as a dormant pupa at Santa Rosa. Furthermore, at the end of the 1978 rainy season, *H. lineata* were common at lights when all other saturniids had become very scarce. These *H. lineata* were the newly emerged second generation that was laying the eggs which would, after surviving the 1979 dry season, produce the 1979 peak in caterpillar numbers.

While rearing *H. lineata* on different host plants in the first half of the 1979 rainy season, I kept records on the duration of the cocoon stage for 59 individuals (Fig. 6). The cocoons were held in screen cages at ambient temperatures equal to those in the nearby forest rich in *H. lineata* cocoons. With males ($n = 28$) the duration was an average of 23.75 days (SD = 4.70; mode = 24, median = 24; range = 13–38). With females ($n = 31$) the pupal duration was an average of 20.74 days (SD = 2.25; mode = 21, median = 21; range = 16–25). The two means are highly significantly different ($t = 3.09$, 57 d.f.). As the larvae were collected from at least 19 different egg clutches, the range of values is probably quite representative of the population as a whole. The differences in pupal duration between the sexes underscores the observation that the exact duration of the pupal stage in these moths is determined by the best duration period (i.e., time of emergence) rather than by some absolute amount of time demanded by physiological processes; the males only weight about 0.2–0.4 as much as do females yet remain in the cocoon three days longer.

Table 1. Dates of emergence of *Hylesia lineata* from cocoons and dates of arrival at lights (1979, Santa Rosa National Park).

Date	Reared from young larvae			From cocoons collected in wild			Arrived at light[a]		
	♀	♂	Σ	♀	♂	Σ	♀	♂	Σ
Jul 6	0	0	0	0	0	0	0	0	0
7	0	0	0	1	0	1	0	2	2
8	0	0	0	1	0	1	0	17	17
9	0	0	0	1	0	1	0	15	15
10	0	0	0	1	3	4	0	11	11
11	0	0	0	2	5	7	0	11	11
12	0	2	2	2	1	3	0	15	15
13	0	1	1	4	7	11	1	20	21
14	1	1	2	5	4	9	1	20	21
15	2	3	5	4	4	8	2	53	55
16	1	0	1	0	4	4	0	16	16
17		2	2	1	2	3	2	44	46
18	6	3	9	1	5	6	0	35	35
19	1	2	3	2	7	9	4	29	33
20	3	0	3	3	8	11	1	16	17
21	2	0	2	1	9	10	1	26	27
22	2	2	4	4	6	10	2	35	37
23	2	0	2	2	4	6	8	76	84
24	1	2	3	0	7	7	14	93	107
25	5	3	8	2	5	7	10	145	155
26	0	0	0	0	12	12	8	127	135
27	3	3	6	3	3	6	7	100	107
28	2	3	5	2	3	5	9	146	155
29	1	1	2	2	1	3	4	96	100
30	0	1	1	0	0	0	7	121	128
31	1	0	1	0	0	0	5	46	51
Aug 1	0	1	1	1	1	2	6	44	50
2	0	0	0	0	0	0			
3	0	0	0	0	0	0	4	12	16
5							1	10	11
8							1	6	7
15							0	1	1
Σ	33	30	63	45	101	146	98	1388	1486

[a] All moths that arrived at the light were captured on the night of arrival.

There are two pieces of evidence which suggest that male larvae become pre-pupae somewhat earlier than do female larvae. First, the average date of cocooning of the males in the previous sample was 27.75 June (SD = 6.39 days; mode = 27 June; median = 27 June; range = 12 June to 8 July) while that of the females was 1.74 July (SD = 5.44 days; median = 1 July; mode = 27 June; range = 23 June to 17 July). These two means are significantly different (t = 2.57, 57 d.f.). Males take 3 days longer in the cocoon stage, but initiate cocooning 4 days earlier than do females, with the result that the peak emergence of the two sexes is strongly synchronized (Table 1). The male and female emergence peaks, though broad, fall into the same time period (11–28 July) in the case of moths reared from larvae and from cocoons collected in the wild. These two samples have very different larval histories yet have the same emergence peaks. This suggests strongly that

both larval and pupal calendars are very well shielded from both temperature and dietary perturbations, since the reared caterpillars were kept in plastic bags on low grade food at a temperature (indoors) that was substantially hotter during the daytime than was the air in the forest.

The equal number of males and females in the sample reared from larvae (Table 1) suggests that the sex ratio of *H. lineata* caterpillars is 1:1. If cocoons are collected in the wild after all larvae have spun, a 1:1 sex ratio should also be obtained. However, if a cocoon collection is made at the time when many larvae are spinning or have just spun, it should be biased in favor of males, since they spin first. The sex of the emergents from wild-collected cocoons (Table 1) shows this clearly. The cocoons were collected on 30 June. Since the average cocoon duration is 21 days for females, and since the forest still had many *H. lineata* caterpillars on the date of cocoon collection, after about 21 July there should have been a more severe decline in the number of emerging females than males, and that is what happened (8 females and 34 males emerged 22–26 July). The final sex ratio was 2.24 males to each female in the 30 June cocoon collection.

Hylesia lineata at Lights

The peak emergence of *H. lineata* from cocoons (July 1979) approximated the peak of adults arriving at lights (a 15 watt blacklight and adjacent 15 watt white fluorescent light hung 1 m above the ground against a white sheet facing into 10–20 year old forest understory 2 m away), but differed in some significant ways. As usual with saturniid moths at Santa Rosa, the *H. lineata* sex ratio of adults at lights was strongly biased in favor of males; there were 14.2 males for each female. The sex ratio of reared material makes it clear that this is not the sex ratio of the moths in the forest.

The numbers of *H. lineata* arriving at the lights per night were greatest between the nights of 23 and 30 July, which was 2–3 days later than the peaks of emergence from reared larvae and cocoons collected in the wild. There are several likely causes for this difference, none of which are mutually exclusive. First, as mentioned earlier, the wild-collected cocoons were taken before all the *H. lineata* larvae in the habitat had spun cocoons, and therefore the sample simply lacked cocoons of the vintage that produced the last part of the peak at lights (on average, the later caterpillars to spin will be the later ones to emerge). Second, the moths at the lights were 1–4 nights old; the more old ones to arrive, the more the peak of arrival at the lights will be shifted later than the peak of emergence from wild-collected cocoons. However, this phenomenon is minimized with saturniids as compared to more long-lived insects since the number of saturniids in the habitat at any one time can be no greater than the sum of the emergences of only a few previous nights.

Seasonal Cycle

At Santa Rosa the life cycle of *H. lineata* is well adjusted to two generations per year (approximately 3 months from egg to egg). However, there is a way that the match of the two cycles with the rainy season may be badly disrupted. If the rainy season begins as early as mid-April, as it does in some years, then the first generation could be pupating by mid-June and laying eggs by mid-July. The second generation would then emerge by late October when the rainy season is still intense.

If the embryos in eggs laid in late October then failed to become dormant (because the rain regime is that of mid-July), they would produce a third generation of caterpillars that would have to complete development on a food resource that is quickly deteriorating and in very dry weather. Such an event might well result in a very low density of *H. lineata* in the following year.

Alternatively, if the rainy season is slow to start (e.g., mid- to late May) the cycles will be displaced forward. Adults will then be ovipositing well into December and the larvae in their eggs should have little difficulty recognizing the cues which signify the beginning of the dry season. Such an event could result in an exceptionally large number of egg nests available at the beginning of the following rainy season.

Fluctuations in Density

H. lineata adults were abundant at lights at the end of the 1978 rainy season in December, but none were taken at lights in July 1978. Also, I encountered only three larvae of this moth while collecting caterpillars of large moths in June of 1977 and 1978 (but several hundred other saturniid caterpillars were found). Egg nests were extremely abundant in the 1979 dry season; hundreds could be found in a day's search. There was a peak emergence in late July 1979 (mid-rainy season). I was absent from Santa Rosa until November 1979, but my Costa Rican field assistant described the forest in late October as being a "living sheet of caterpillars of *H. lineata*". When I arrived at the beginning of November, standard food plants like *Casearia corymbosa* were largely leafless and the foliage of the forest was festooned with the corpses of *H. lineata* caterpillars that had been killed by a virus (see below). *H. lineata* adults were, however, moderately abundant at the lights in late November and early December 1979 (a maximum of 11 males were taken in one night at the same light which attracted so many in July 1979 (Table 1)). Careful search of foliage located 16 egg masses in December 1979. During two weeks in March in the 1980 dry season, intensive search of the vegetation in the Park resulted in 18 more egg nests. This amount of searching would have yielded thousands of egg masses in March or July 1979. Collection of all saturniids at three different lights on every night of the 1980 rainy season produced a total of 26 males and no females of *H. lineata*. Caterpillars of *H. lineata* were encountered on three occasions in the same forest in which I had estimated a density of one last instar larva per 4 m² in June 1979 (see Janzen, 1981). Intensive searching for 10 days in March in the 1981 dry season yielded no egg nests. In June–July 1981, intensive collecting of caterpillars located two single *H. lineata* caterpillars and one group of six (on *Casearia corymbosa* and *Muntingia calabura*). Despite intensive collecting at 2 or 3 lights almost every night through June, July and August 1981, only two males and no females of *H. lineata* were taken at lights. Two female *H. lineata* were reared and placed out in screen cages in late July 1981; they called each night for the three nights until they died, and they attracted no males (nor were any males taken at lights those nights). On two of the nights that a female was put out to call, she was at the exact place where in July 1979 I encountered 16 egg nests on one branch of a hapless *Casearia corymbosa*. *Note added in press*: The same low density of *H. lineata* at Santa Rosa has occurred during the 1982 and 1983 rainy seasons.

Hylesia has a well-deserved reputation for occurring in large numbers in certain

years. Of *H. nigricans* Berg, Draudt (1929) stated that it is "officially declared a vermin in the Province of Buenos Aires and often strips wide stretches of willows and other plantations .... A few years ago the insects were in such immense numbers in the willow plantations near the city that the droppings were to be heard drizzling to the ground like rain" (p. 760). The enormous numbers of adults which sometimes appear at lights and generate outbreaks of lepidopterism (outbreaks of rashes in humans caused by moth hairs in the air) in neotropical countries must have been generated by even larger numbers of caterpillars.

Predators and Parasitoids

Although *H. lineata* has a number of protective traits, it is fed on by other animals. During the 1979 dry season, when egg nests were conspicuous and abundant, I frequently found nests that had been torn open by a bird and the eggs mostly removed. Climbing rodents may also have contributed to this egg predation, but in contrast to bird beaks, their teeth do not leave a diagnostic imprint on the soft felt covering around the eggs.

The eggs were intensely parasitized by a very small hymenopteran (*Anastatus furnissi* Burks., Eupelmidae). The adult wasps emerged from the eggs only a few weeks after they were laid. The adult wasps cut numerous round minute exit holes through the felt covering surrounding the eggs. For several reasons, I suspect that the eggs were parasitized by this wasp just at the moment that the eggs were being laid. First, egg nests collected in the dry season a month or more after being laid in late December 1978 often had parasitoid exit holes but never produced parasitoids at a later date. Second, the felt covering around the eggs probably blocks the adult wasps' access to the eggs (these minute wasps lack an ovipositor of sufficient length to reach the eggs through the felt). Third, the eggs should be easiest to locate at the moment of oviposition, since fluids vaporizing off their surface could be used by the wasp as an odor cue to locate the eggs. It is even possible that the wasps use the pheromones released by the female moth to locate her, and are phoretic on her until she begins oviposition (R. S. Peigler, pers. comm.).

Winder (1976) noted that Brazilian egg masses of *Hylesia* prob. *fulviventris* were "often partially or wholly parasitized by the microhymenopteran, *Telenomus* sp. (Scelionidae)". He also reared *Belvosia brasiliensis* from the larvae (see below).

The larvae of *H. lineata* are probably not subject to severe predation by any vertebrate even when the larvae are abundant, since they urticate severely in all instars. All hemileucine saturniid larvae are urticators (see Zikan, 1927 for a drawing of the urticating spines of *Hylesia*), and the larvae of other species of *Hylesia* are notorious for being severely urticating (Marsh and Pinango, 1971; Quiroz, 1978; Frazer, 1965; Rothschild et al., 1979; Picarelli and Valle, 1971; Arocha-Pinango and Layrisse, 1969). However, while *H. lineata* caterpillars are extremely painful urticators, I have experienced no long-term bad effects from repeated urtications. At Santa Rosa, probably the only vertebrate that would feed on *H. lineata* would be the squirrel cuckoo (*Piaya cayana*: Cuculidae). They have the reputation of grabbing an urticating larva by one end and repeatedly bashing it against a branch, apparently breaking the spines and rendering them ineffective, before eating it. I have found *Automerus zugana* Druce last instar larvae in the gizzard of a squirrel cuckoo at Santa Rosa (unpubl.).

The 4th to 6th instar larvae of *H. lineata* are either light green or gray-black (Fig. 7). Such polymorphism implies the existence of a visually-orienting predator. The larval habit of living in small nests in the daytime may offer a clue. If they are preyed on at this time by some vertebrate that peers into the nests or tears them partly open, such as the squirrel cuckoo mentioned above, the predator will have difficulty seeing the light green morph against the green leaves if the nest interior is well illuminated. However, I have found that if the nest is dark inside, the gray-black caterpillars are much harder to see and the predominantly green caterpillars stand out against the shadows and the dark caterpillars.

If 4th to 6th instar *H. lineata* caterpillars are collected in the wild in Santa Rosa, the same genera of parasitoids emerge from them as I have reared from a number of other species of saturniids in Santa Rosa. For example, *Belvosia bella* G. T. (Tachinidae: Goniinae) and other tachinids, and an unidentified species of *Enicospilus* (Ichneumonidae: Ophioninae) were reared from *H. lineata* during the 1979 population peak. Both *Belvosia* and *Enicospilus* emerged as adults from the *H. lineata* cocoons. I cannot estimate the severity of parasitoid attack, but less than 10% of the caterpillars had parasitoids when collected in the 4th to 6th instar, whether in the 1979 peak density year or in other years.

As mentioned earlier, an undescribed polyhedrosis virus disease (R. Granados, pers. comm.) killed most of the caterpillars in the second half of the 1979 rainy season. They all died in the same pose: holding tightly with the prolegs and the anterior half of the body hanging free of the substrate.

I occasionally encountered cocoons that had been ripped open by an unidentified vertebrate and had the pupa removed. Caged *Liomys salvini*, the common forest-floor heteromyid seed-eating rodent (Bonoff and Janzen, 1980) in Santa Rosa, eagerly eat the naked pupae of *H. lineata* just as they do all other saturniid pupae except those of *Dirphia*, *Periphoba* and *Arsenura armida*.

The adults' susceptibility to predation varies with their sex. Living male and gravid female *H. lineata* were offered to a taste panel of the small rodents *Oryzomys palustris* and *Oryzomys caliginosus* (Cricetidae). The moths were mixed in with a variety of insects known to be highly edible to these individual rodents. Female *H. lineata* were invariably rejected undamaged after capture by the rodents, but males were eaten in numbers related to the hunger of the rodent (W. Hallwachs, pers. comm.). For example, on 25 July 1979, a 60 g *O. caliginosus* that had not been fed for 24 hours caught and ate 37 male *H. lineata* released one at a time into his cage; a female *H. lineata* was dropped into the cage along with each male, and all females were rejected. If the moths were offered one at a time in a well-lit cage, the rodent could distinguish males from females at a distance of 20 cm. It would not move from its resting position to take a female moth but instantly darted to the male moth over the same distance. However, in other feeding trials where *H. lineata* were offered alternatively with large grasshoppers and cryptic butterflies, after eating 2–11 male *H. lineata* the rodent stopped eating them but continued to feed on the other insects. In all cases of feeding, the rodents ate the thorax and abdomen of the male *H. lineata* and discarded the wings.

When an inexperienced rodent was offered a male *H. lineata*, the moth was killed by biting and consumed with no sign of discomfort. The abdominal hairs of the males (Fig. 8) show no modifications that suggest they might be urticating. However, when the same rodent was offered its first female moth, the response
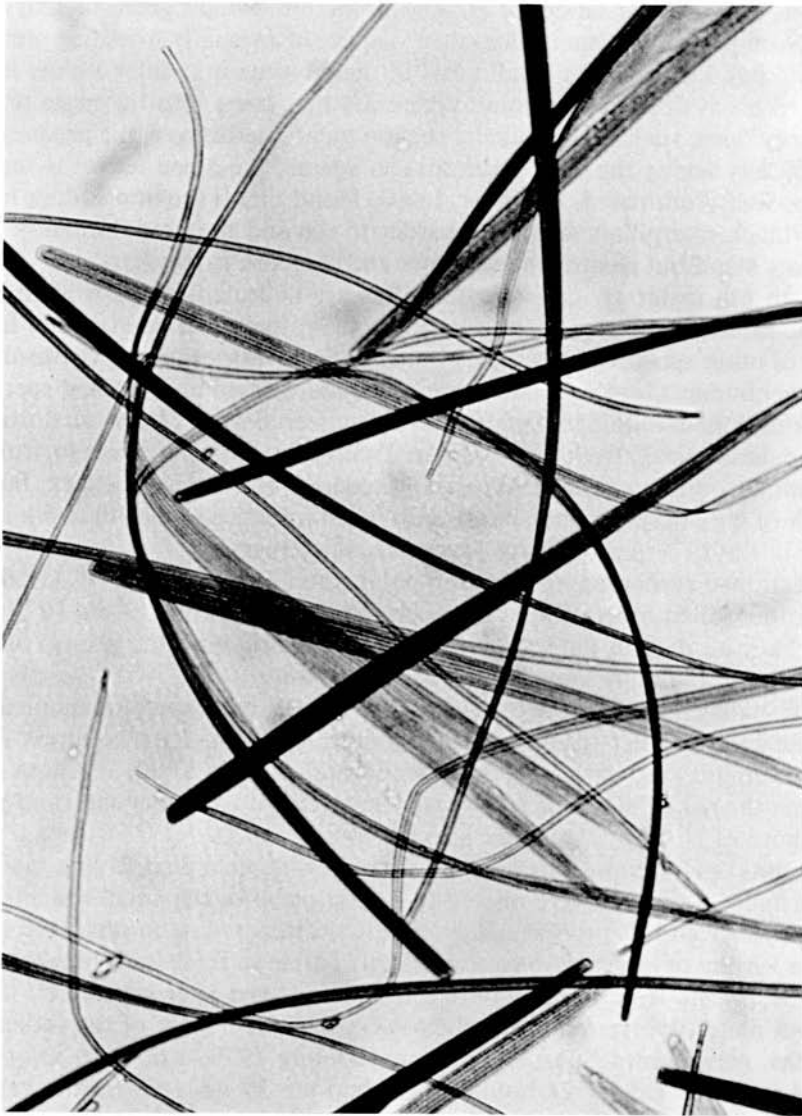
Fig. 8.   Representative abdominal hairs (scales) from a male *H. lineata* (125×).

was very different. It was grabbed, bitten, and almost immediately rejected. This was followed by several seconds to minutes of facial cleaning. The rodent's attack caused the release of some of the long yellow hairs from the abdomen, and the mouse may well have been removing these. However, it also acted as though some finer material was in its nose, mouth or eyes, material that elicited strong scratching and rubbing. I assume that this response was due to irritation by the many short needle-like hairs occurring as "underfur" on the female abdomen (Fig. 9a, b; and see EM figures in Lamy et al., 1982; Lamy and Lemaire, 1983). These short hairs cause an intense burning and itching sensation on my skin if
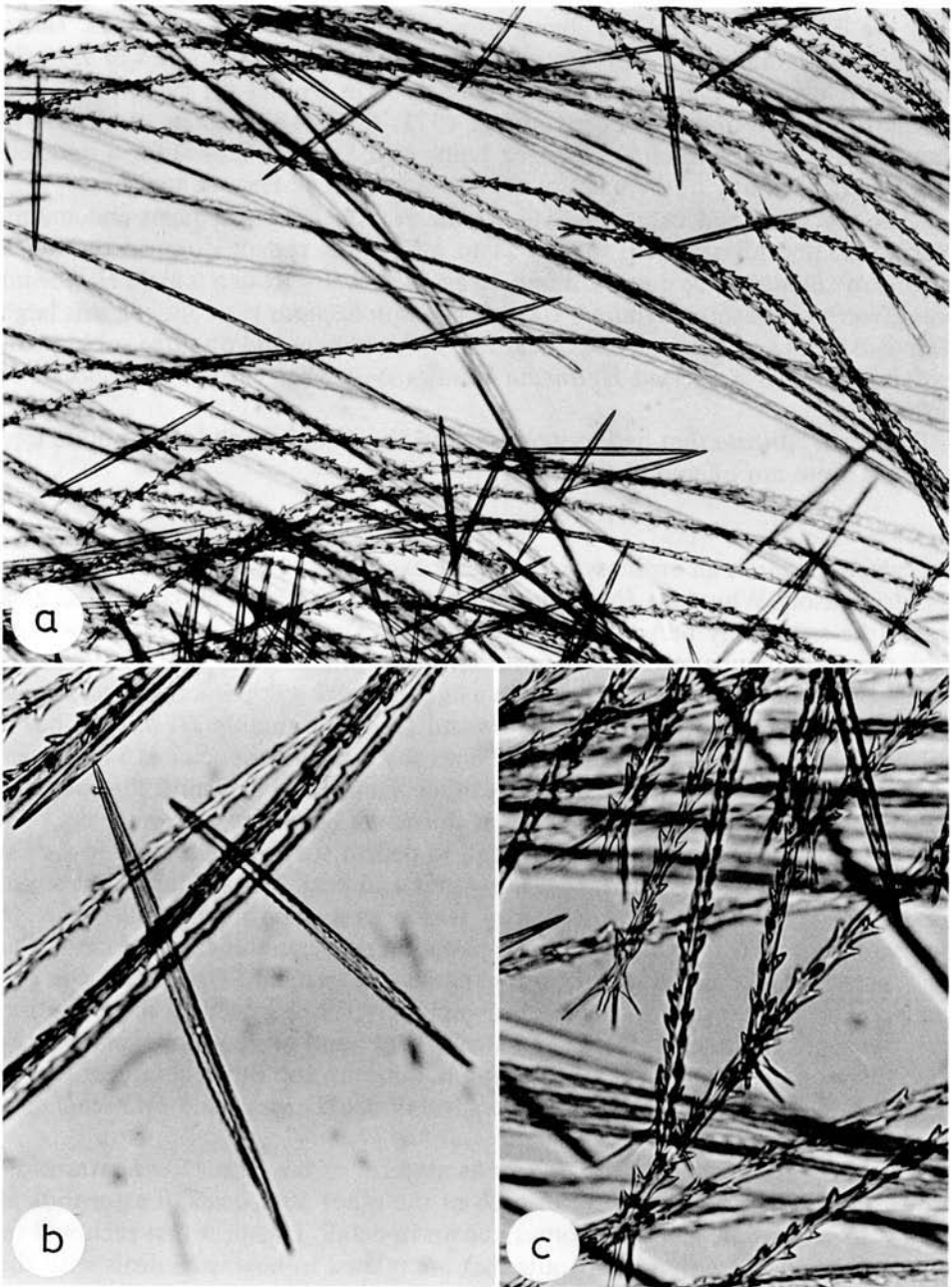
Fig. 9. a. Abdominal hairs (scales) from a female *H. lineata* (50×). A mix of these hairs forms the felt around the egg mass (Figs. 2, 4, 5). b. Short urticating hairs (scales) from Fig. 9a (note barbs on lower ends) (125×). c. Modified felt-forming ends and barbs of long abdominal hairs (scales) from Fig. 9a (125×).

they are rubbed on, even after being preserved in alcohol for two years. Hairs from the abdomens of South American females of the other species of *Hylesia* are well known to be human irritants (Quiroz, 1978; Hill et al., 1948; Pesce and Delgado, 1971; Winder, 1976; Rotberg, 1971; Ruhl, 1923; Zaias et al., 1969; Lamy et al., 1982; Crotch, 1956). See Lamy and Lemaire (1983) for a detailed morphological study of the hairs of *Hylesia* adults as systematic tools.

Once a rodent had experienced a female *H. lineata,* subsequent encounters usually elicited no attack; if there was an attack, the rodent dropped the moth before any damage was done. On one occasion at Santa Rosa a female *H. lineata* was given to a presumably naive 100 g *Sigmodon hispidus* (Cricetidae); this large native rodent ate the thorax and discarded the abdomen, and on three subsequent evenings, it always rejected *H. lineata* females even when eating other species of insects.

Female *H. lineata* that had oviposited, and therefore had abdomens quite free of hairs, were not offered to the mice.

Discussion

Hylesia lineata is an ordinary hemileucine except for the way in which it passes the dry season. Why does *H. lineata* not pass the dry season at Santa Rosa as a pupa (the same may be so for *Hylesia dalina*)? The answer may be associated with the normal pupation site of hemileucine saturniids. All tropical hemileucines whose pupation site is known pupate in a light to tough silk cocoon among foliage or the upper layers of the litter. *H. lineata* (and presumably *H. dalina*) has a substantially smaller (lighter) pupa than does any other hemileucine at Santa Rosa (it is also smaller than the pupa of any other Santa Rosa saturniid that pupates above the soil surface). It may be that at this small body size, the water reserves and volume to surface ratio are too small to permit survival of a pupa in a light cocoon fully exposed to the dry season winds and heat. For a saturniid as small as *Hylesia* to pass the Santa Rosa dry season as a pupa might well require a deviation from the normal hemileucine pupation mode; in this case, the deviation was instead in the direction of producing an egg nest that could pass the dry season. The same problem could conceivably have been solved by the evolution of a pupal cuticle less permeable to water, a larger and more water-rich pupa, or the behavior of pupating in the soil (as is done by the other small saturniids (Ceratocampinae) in Santa Rosa, *Adeloneivaia isara* (Dognin) and *Ptiloscola dargei* (Lemaire)).

It is tempting to think of *H. lineata* as atypical of the Santa Rosa saturniids. However, as the natural history of each of the other 30 species of saturniids at Santa Rosa (Janzen, 1982a) becomes known in detail, I suspect that each will be found to have its own peculiar traits that are related to how each deals with the challenges of living in a highly seasonal habitat rich in plant species.

Acknowledgments

Camazine aided in photographing the body hairs and in locating references. C. Lemaire identified the moth; I dedicate this paper to his enthusiastic interest in understanding saturniid systematics.

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