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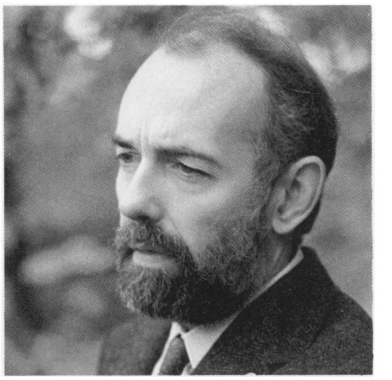

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When, and when not to leave

The tropics are very seasonal. There are times of year when the carnivores are more numerous, when there is more sun, when food is more scarce, when there is more rain. Many tropical plants and animals sit tight and tough out the hard times by being unreproductive or dormant. But many tropical animals get up and move to more hospitable localities when unfavorable seasons come along. Such local seasonal movements have long been apparent to tropical field naturalists and rural residents. In a tropical dry forest, for example, many butterflies, bugs, beetles, lizards, monkeys and birds move into moist and semi-evergreen lowlands and riparian understory vegetation during the dry season. Then, when the rains come, the lowland forest understory becomes a shadow desert and the animals move back onto the sunny hillsides where the food is. But we have long been oblivious to a much more dramatic kind of movement in the tropics.

Central America, like many tropical land masses, has a north–south mountainous backbone. Its eastern side is bathed by the moist tradewinds, and supports or supported a lush rain forest vegetation. On the other hand most of its western side is in a rainshadow, receiving rain only during the half of the year (May through November); during this rainy season the sun is relatively overhead and the land mass heats up enough to pull in moist air from the Pacific Ocean. The western dry forests are subject to a 4–6 month rain-free dry season that is in many respects equivalent to an annually recurrent desert. These forests are fully to partly leafless during much of the dry season, and are nearly free of leaf-eating insects as well.

While almost all of Central America's western dry forests have been severely converted to fields and pastures, and are roasted almost annually by man-set fires, in a few places forest fragments remain and have conservation status. One of these places is Santa Rosa National Park, 108 km^2 in area, in northwestern Guanacaste Province, Costa Rica. In late April or early May, the first towering columnus clouds appear on Santa Rosa's southern horizon, and every day the rainy season draws nearer. Then late on an almost unbearably hot day, the first rains fall, and the forest turns soggy-moist and cool. If a blacklight is placed out in the forest, innumerable insects appear at the light; moths and beetles are the most prominent. For several months after this, insects are abundant at the lights and the newly foliated world is food for multitudes of species and individuals of chewing and sucking insects, which are in turn food for diverse and numerous carnivores. Caterpillars are everywhere, as are the birds, mammals, spiders, scorpions and insects that eat them. The rainy season continues, with breaks and periodic droughts, through November. Then the winds and rain-free heat differentially dries Santa Rosa's varied habitats until the beginning of the rainy season in the following year.

We have long viewed the myriads of insects that appear at Santa Rosa's lights at the time of the first rains as having newly emerged from dormant pupae; indeed, many of them have. Such a view continues a venerable tradition of regarding the beginning of the rainy season in a strongly season tropical climate as a time of mass insect emergences. But there is something wrong. All the observations do not quite fit the scenario of mass emergence from pupae. Three discrepancies are very prominent:

1) If the first rain falls, say, between 4 and 6 pm, tens of thousands of moths come that night to a light that was visited by only a few hundred moths the night before; these moths certainly did not have time to be cued by the rain, emerge from pupae and harden their wings between the rain and sunset.

2) If caterpillars are reared to the pupal stage in an open-air laboratory during the rainy season, the pupae of many species then eclose within a few weeks, rather than remain dormant. In the forest, the newly emerging conspecifics then disappear from the habitat during the later part of the rainy season and the following dry season; there is no sign of caterpillars or pupae of these species in the habitat – in addition, their adults only rarely, if at all, appear at the lights or are encountered in the forest.

3) The adults of some of the species of moths that appear in Santa Rosa at the first rains are a different size than are their offspring that emerge from pupae and disappear several months later.

The emerging puzzle has two other salient parts. An ongoing inventory of Costa Rica's moths shows clearly that many species of "Santa Rosa" and "dry forest" moths also occur in Costa Rica's lowland rain forests. Second, when lights are placed at high elevations (1500–3000 m) in the mountainous backbone that separates the wet and dry sides of Costa Rica, many species of moths that breed in Santa Rosa and are common on both sides of the country are caught at these lights. Neither the larval host plants of these moths nor close relatives of their host plants occur at these high elevations.

A scenario

A dry forest patch, such as Santa Rosa National Park, does not exist unto itself. The circumstantial evidence suggests the following scenario of cross-Costa Rica seasonal migration of moths. The large moths in the family Sphingidae offer the most unambiguous examples. (Sphingids are well known around the world as the moths that look like little hummingbirds and visit fragrant white, purple or blue flowers at dawn, dusk or after dark to drink nectar with their very long tongues.)

During the first several weeks of the rainy season at Santa Rosa (late April through May), at least 30–40 species of sphingids (of the genera *Erinnyis, Eumorpha, Aellopos, Perigonia, Pseudosphinx, Cocytius, Xylophanes, Neococytius, Manduca, Pachylia, Pachylioides, Hemeroplanes, Sphinx, Cautethia,* etc.) arrive, presumably flying in from wetter and greener parts of Costa Rica. They are joined by another 8–12 species that have been present as dormant pupae below ground (mostly *Manduca*) and a few species (mostly *Amplypterus, Protambulyx, Pachylia*) that have somewhat continuous generations on evergreen host plants. All seek out their newly leafed-out host plants and each female lays a few eggs per night on the new foliage during the first 3–6 weeks of the rainy season. The sphingid caterpillars (which are extremely abundant in June and early July) grow rapidly for 3–6 weeks and then pupate. The adults of those species that arrived from outside the park then emerge from their pupae in July and August, and most individuals disappear, presumably leaving the park. A few remain and attempt a second generation in Santa Rosa. Of those species that were present as dormant pupae when the rains began, some species remain dormant as pupae and some emerge to attempt a second generation. By the end of the rainy season, about the only sphinx moths that are left in the habitat are those very few species in which a few members continue to breed as long as there are leaves on their hosts. During the six month dry season, the park is almost free of sphingid adults.

Assumption of this pattern of cross-country seasonal migration allows a broader understanding of sphingid biology throughout Costa Rica. Why do sphingids that have larval host plants at sea level arrive at lights at 2500 m elevation? They are newly emerged adults crossing from the dry forests of the western side of Costa Rica to the eastern rainforests, or the reverse. Why are these moths at high elevation blacklights represented by a 50:50 sex ratio, while at lowland blacklights males outnumber females by more than 10:1? In both cases moths arrive at the light because they are using it as a landmark during long flights; in the lowlands the males are caught while searching for females, while in the highlands both sexes are caught because both migrate. In the park tens of male sphingids arrive at the light for each female to arrive. Why are there so many species of sphingids in common between the rain forest and the dry forest? Because many Costa Rican sphingids count both the wet and dry forest as their habitat, even within a single generation; furthermore, when such migratory species are in the dry forest, they are there in the rainy season, a time when the wet and dry sides of Costa Rica are minimally different.

How can many species of sphingids appear at the lights as soon as the first rains begin (or even, sometimes, a few days before)? Because they are flying in from outside rather than depending on the rain to stimulate the final stages of pupal development or moisten the soil sufficiently for them to escape from belowground pupal chambers. Why are migratory parents of Santa Rosa's first generation larger than their immediate offspring? Because the incoming moths were raised in the rainforest; they are the (grand?) children of those that left Santa Rosa the year before and they were reared on a diet of rain forest host plants. Why do they emerge from their pupae in the middle of the rainy season, yet then disappear from Santa Rosa? Because they have only one generation a year (with no extended pupal dormancy) in the dry forest, and then migrate to a different habitat for subsequent generations.

But why do they leave Santa Rosa? There are several interrelated reasons. In the dry season, the old foliage largely disappears and new foliage is not produced. Also, the air is extremely dry and direct insolation very hot; both conditions are tough on caterpillars, and especially the young ones. But such an answer, based on the obvious harshness of the dry season for leaf-eating caterpillars, begs the question of why so many species of sphingids leave (or become dormant pupae under the ground) after having only one generation during the first half of the rainy season; during the second half of the rainy season, their hosts stand fully leafed and many even continue to produce new foliage. Food is apparently available and the climate hospitable for caterpillars. Two potential answers come to mind. The foliage chemistry is unacceptable during the second half of the rainy season, or carnivore pressure is increased in comparison with the early rainy season. Feeding tests and leaf chemistry measurements done to date suggest that there is no difference in the chemistry of sphingid host plants between the first and the second half of the rainy

season. Furthermore, the few individuals of sphingid caterpillars that are present in the second half of the rainy season grow quite normally on their host plants.

The answers lies in the carnivores. The dry season is the hard time for insect-eating carnivores, be they predators – such as birds or spiders or wasps – or parasitoids such as ichneumonid wasps and tachinid flies. Their density is maximally low when the rains begin, owing to population decimation and lack of reproduction throughout the previous nine months; even those that have been dormant along with their hosts from the previous rainy season have suffered conspicuous mortality. But the carnivore community grows fat and multiplies on the (very large) first generation of caterpillars (all species). At the end of this first caterpillar generation, there are newly fledged birds and mammals, and multitudes of newly emerged carnivorous insects. The newly emerging female sphingid (or other moth) finds herself faced with the choice of ovipositing into an environment that is about as rich in carnivores as a tropical habitat can be, or leaving in search of less dangerous habitats.

The presentation of such a choice to the female moth begs the question of why she ever comes to Santa Rosa in the first place. Why do sphingids reared in the rain forest leave the rain forest? While the rain forest is not a friendly place – it has its full share of carnivores ready to eat caterpillars – I suspect that it is on average more dangerous than is the dry forest at the beginning of the rainy season. Even the tiny carnivores, the disease organisms, are at their lowest density on the new foliage at the beginning of the rainy season. However, by the end of the first generation of caterpillars in the dry forest, enough carnivores (and disease inocula) have been generated by it to render the dry forest substantially more dangerous than is the rain forest at any time of year.

Such a hypothesis questions whether the populations of many of these species of sphingids would survive if all generations were restricted to rain forest (such as would have been the case before Costa Rica's relatively recent mountain backbone appeared). In other words, does a sphingid population greatly increase during the dry forest generation, then gradually decline in the rain forest until it is rejuvenated by a new pulse of adults in the following rainy season in the dry forest? The answer may even be confounded by a portion of the population staying in the rain forest rather than migrating over to the dry forest at the beginning of the rainy season.

A vision of sphingid moths moving back and forth across tropical Costa Rica, just as birds move back and forth between North American forests and Latin American forests, brings to mind many processes about migrants. The sphingids are major pollinators of vines, shrubs, epiphytes and treelets in both rain and dry forest; the elimination of either end of their migratory route, or the part in between, will have highly negative effects on those portions of the multiple interactions of sphingids with these plants. Just as many tropical habitats are heavily occupied by stray plants, plants that have originated in breeding populations in other habitats, rain and dry forest is rich in volant migrant animals that originate in other habitats.

Do insects other than sphingids make the migratory trip? All of the observations that have led to proposing the scenario outlined for sphingids apply also to numerous species of Santa Rosa moths in the families Noctuidae, Pyralidae, and Notodontidae. Many Santa Rosa butterflies show the same seasonal pattern of breeding and movements as postulated above for the sphingids. There are massive movements of tachinid flies out of Santa Rosa's dry forests about the same time that Santa Rosa's sphingids leave in the middle of the rainy season.

How do sphingid moths know when to move and what guidance systems do they use? How did such a migratory pattern evolve? Why don't all of the Costa Rican sphingids individuals and species make such movements? Are the migratory species just rain forest moths that are making use of a seasonal pulse of food in a relatively safe habitat in the dry forest, or are they dry forest moths taking shelter from their enemies and harsh dry season conditions when they move to the rain forest? Today, dry forest is greatly reduced to a few patches; do the incoming migrants from the rain forest simply get lost or are they able to locate these patches of relatively suitable habitat? Do these small patches of dry forest generate today as many moths to service rain forest plants and be eaten by rain forest carnivores as did the once extensive areas of dry forest? Must the flyway between also be conserved, thereby placing a premium on dry forest parks that join directly to rain forests that migrants can move to and from?

Whatever the answer to questions like these, cross-tropical seasonal migration is a fact. A tropical dry forest national park cannot exist unto itself. It must exist in consort with the rain forest vegetation that is the recipient and generator of the migrants.

D. H. Janzen, Dept of Biology, Univ. of Pennsylvania, Philadelphia, PA 19104, USA.