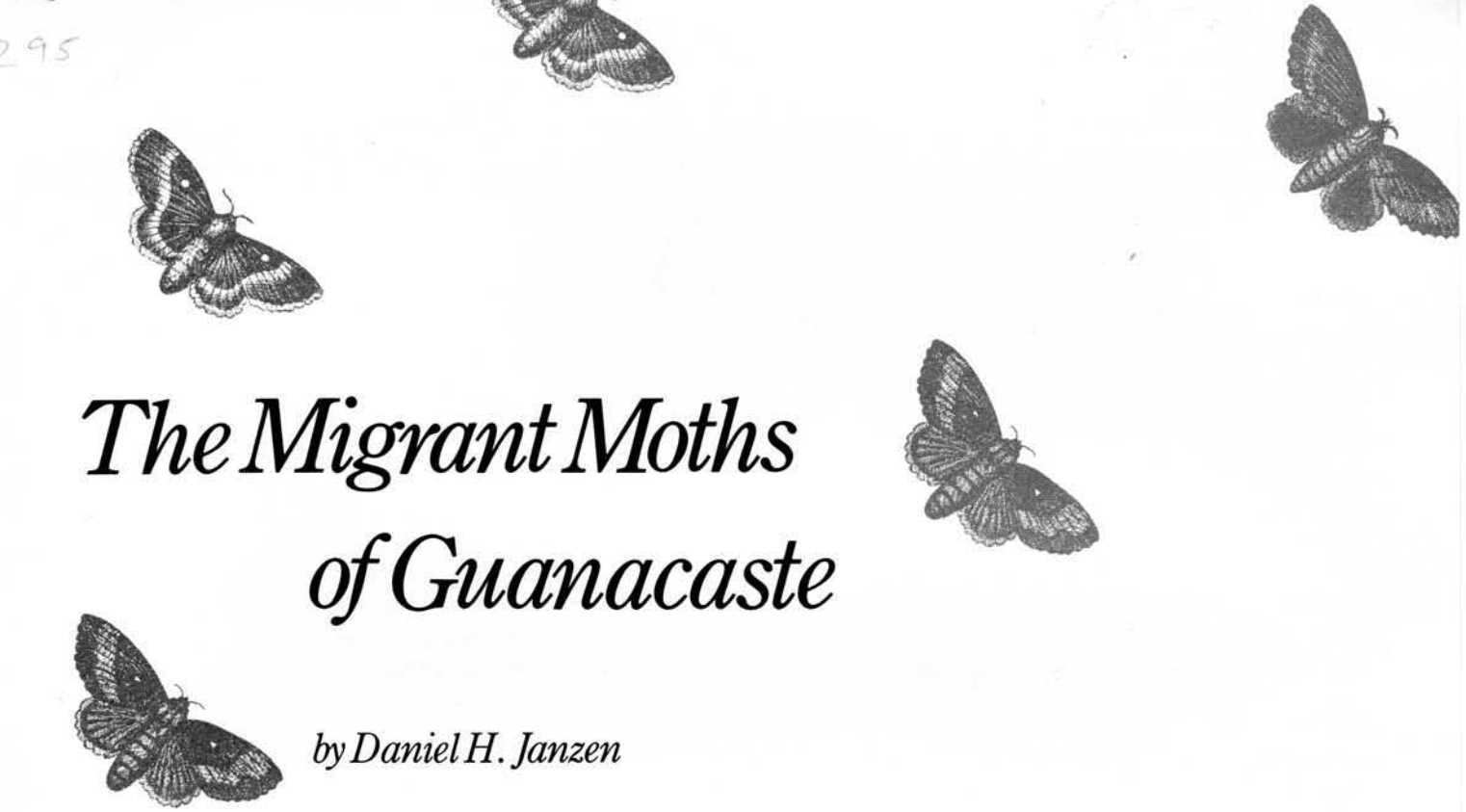

The Migrant Moths of Guanacaste

by Daniel H. Janzen

The tropics are subject to seasonal extremes. There are times of year when the weather is harsh, when food is scarce, when there is too much sun, or too much rain. Many tropical animals tough out the hard times by sitting tight and becoming dormant or unreproductive. But other species get up and move to more hospitable localities. In a tropical dry forest, for example, butterflies, beetles, lizards, monkeys, and birds concentrate in the moist and semi-evergreen lowlands and riparian vegetation during the dry season. Then, when the rains come and the lowland forest understory becomes shaded over, the animals move back onto the sunny hillsides, where the food is. Such local seasonal movements have long been apparent to tropical field naturalists. But we are just beginning to learn about a much more dramatic kind of seasonal migration.

Central America, like many tropical land masses, has a north-south mountainous backbone. Its eastern side is bathed by the moist tradewinds and supports a lush rain forest vegetation. Most of its western side lies in a rain shadow, receiving a rainy season only during the half of the year when the sun is directly 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 four-to-six-month dry season that creates what is in many respects an annually recurrent desert.

For the past fourteen years, I have been doing research in one of Central America's few remaining dry forests, at Santa Rosa National Park, in Guanacaste Province on Costa Rica's Pacific coast. During much of the dry season here, the forest is fully to partly leafless, and there is an extreme paucity of leaf-eating insects. Then, in late April or early May, the first towering cumulus clouds appear on the southern horizon. Day by day the rainy season draws nearer. Late one afternoon, on an almost unbearably hot day, the first rains fall, and the forest turns soggy-moist and cool. The newly foliated world is food for multitudes of chewing and sucking insects of many species. Suddenly, caterpillars are everywhere, as are the birds, mammals, spiders, scorpions, and insects that eat them.

As part of our research activities during the rainy season, Winnie Hallwachs and I have been placing electric lights in the forest at night, to attract flying insects which we then identify as to sex and species. Each night's catch includes a feast of sphingid moths, the insects I specialize on. Sphingids are well known around the world as the moths that look like little hummingbirds and visit fragrant flowers in the night or dusk to drink nectar with their very long tongues.

We have long viewed the myriads of insects that appear at the time of the first rains as emerging from dormant pupae, as indeed many of them are. But there is something wrong with this explanation—it does not account for all the observations. There are three prominent discrepancies:

1. If the first rain falls, say, between four and six p.m., that evening there may be tens of thousands of moths arriving at a light that was visited by only a few hundred the night before; these moths certainly did not have time to emerge from pupae and harden their wings between six p.m. and dark.

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2. During the rainy season, moths of many species emerge from the pupal stage to become active adults and then disappear; during the later part of the rainy season and the following dry season, there is no sign of their caterpillars or pupae in the habitat, and adults only rarely appear at the lights.
3. Some of the moths that appear with the first rains are different in size from their offspring that emerge from pupae several months later.

The puzzle has two other salient parts. An ongoing inventory of Costa Rica's moths shows clearly that many species of "Santa Rosa" moths also occur in lowland rain forests on the eastern side of the country. Second, when we have placed lights at high elevations—1,500 to 3,000 meters—in the mountainous backbone that separates the wet and dry sides of the country, many species of lowland moths are caught at these lights. However, the host plants of their caterpillars do not occur at these high elevations.

These observations suggest that the earlier explanation for the sudden abundance of moths at the beginning of the rainy season is incorrect, and that at least some species of moths migrate seasonally between the wet and dry sides of Costa Rica. The large moths in the sphingid family offer the most unambiguous example. The circumstantial evidence points to the following scenario:

During the first several weeks of the rainy season at Santa Rosa, at least thirty to forty species of sphingids arrive in the park, flying in from wetter and greener parts of Costa Rica. They are joined by another ten to fifteen species that have been present as dormant pupae below ground and a few species whose caterpillars have been living on evergreen plants. All seek out the newly foliating plants and each female carefully places her eggs, a few per night, on the new leaves. The caterpillars grow rapidly for three to six weeks, and then pupate. The adults emerge from the pupae in July and August, and individuals of those species that arrived from outside the park then leave. By the end of the rainy season, only a very few species of sphingid moths are left in the habitat, a few members of them continuing to breed as long as there are leaves on their host plants. During the six-month dry season, the park is almost free of sphingid moths.

Recognition of this pattern of cross-country seasonal migration answers many questions about sphingid biology throughout Costa Rica.

What are the sphingids doing that arrive at lights placed at 2,500 meters elevation, yet whose larval host plants do not occur anywhere near these elevations? They are newly emerged adults, flying from the dry forests of the western side of Costa Rica to the eastern rain forests, or the reverse.

Why are these moths at high elevation represented by a 50:50 sex ratio, while in the lowlands, tens of male sphingids arrive at the light for each female? Because both sexes make the cross-country trip. In the lowlands, the lights catch the males while they are searching for females, using the lights for landmarks. A light aids them to fly in a straight line, at right angles to the wind that carries the sex pheromone released by the female. When the male encounters the sex pheromone, it turns and flies upwind to the female. Females have no use for lights as guides in their search for host plants, because they fly from plant to plant, checking each one.

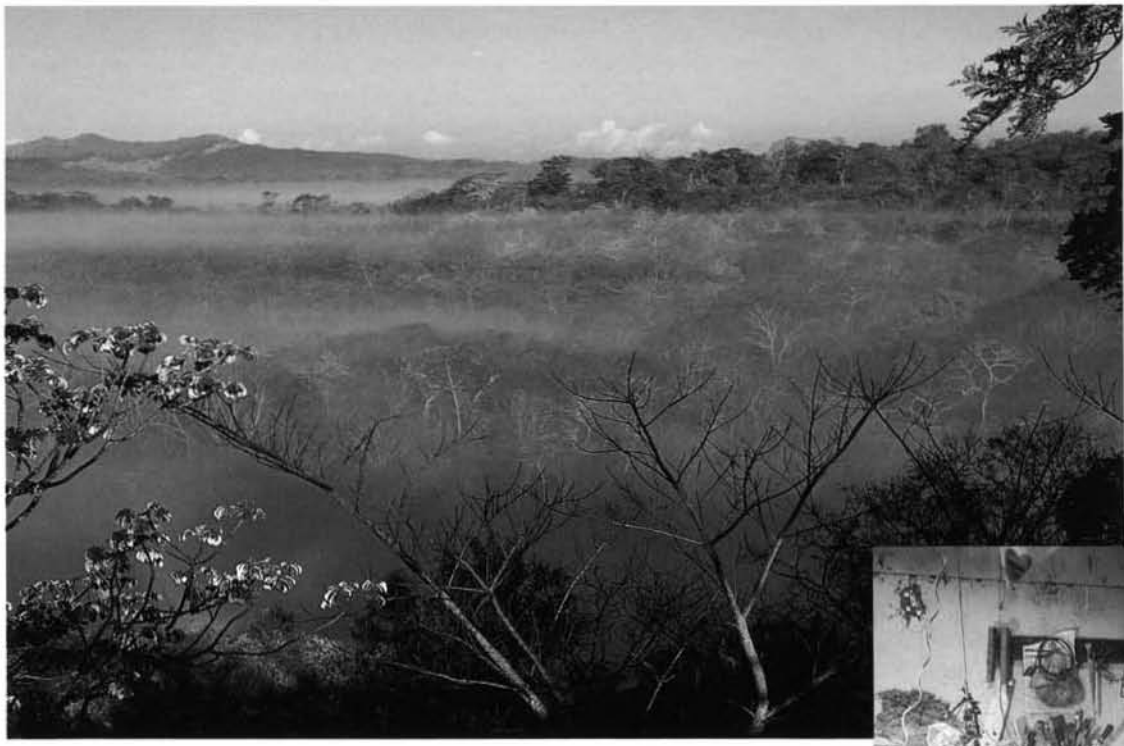
Why are there so many species of sphingids in common between the rain forest and the dry forest? Because many Costa Rican sphingids are migratory on an east-west vector; they count both the wet and dry forests as their habitat, even within a single generation. Furthermore, such migratory species come to the dry forest during the rainy season, a time when the wet and dry sides of Costa Rica are minimally different.

How can sphingids appear at the lights in Santa Rosa as soon as the first rains begin (or sometimes even a few days before)? Because these moths are flying in from outside, rather than emerging from dormancy below ground.

Why are the new arrivals at the beginning of the rains different in size from those of the same species that emerge after the first generation in Santa Rosa? Because incoming moths are the (grand?)children of those that left Santa Rosa the year before; they grew up on a different diet, one of rain forest plants.

Why do moths leave Santa Rosa? There are several interrelated reasons. During the sixth-month dry season, the old foliage largely disappears and new foliage is not produced. The air is extremely dry and the direct sun very hot. These are unfavorable conditions for caterpillars, especially young ones. But why do so many species leave during the first half of the rainy season, after only one generation, when their host plants are still fully leaved? The answer lies with the carnivores. The population of insect-eating carnivores—be they predators such as birds or spiders or wasps, or parasitoids such as ichneumonid wasps and tachinid flies—is at its lowest when the rains begin. The long dry season is hard on these carnivores. The first generation of caterpillars offers a large source of food on which the carnivore community fattens and multiplies. At the end of this first caterpillar generation, the sphingid moth is sharing a habitat with many newly-fledged insectivorous birds and mammals, and a multitude of new carnivorous insects. The emerging female sphingid is faced with the choice of laying her eggs in a very dangerous environment or leaving in search of one with fewer carnivores.

But why does the female moth ever come to the dry forest in Santa Rosa in the first place? Why leave the rain forest? The rain forest is no friendly place for sphingids. 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 in the first part of the



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Early morning fog during the dry season in the dry forests of Santa Rosa National Park, a sector of Guanacaste National Park on Costa Rica's Pacific coast.

Daniel Janzen recording data on moth biology in the living room of his home in Santa Rosa National Park.

Estación Mengo, a biological station in the wet forest end of Guanacaste National Park where the migrant moths spend the dry season.

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The sphingid moth Xylophanes pluto, *sleeping on a leaf. This is one of the species that migrates into Santa Rosa National park at the beginning of the rainy season, has two generations, then leaves the park for the rain forest during the dry season.*

rainy season. The dry forest also has the advantage of being rich in new (and disease-free) foliage at the beginning of the rains. However, by the end of the first generation of caterpillars in the dry forest, the carnivore population has increased to the level where this habitat is more dangerous than is the rain forest.

Assuming this scenario is correct and we have identified a hitherto unknown migratory pattern among sphingid and other moths (all of the observations that have led to the scenario for sphingids apply also to numerous species of Santa Rosa moths in other families), the explanation still leaves many questions unanswered. 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 make such movements? If the dry forest habitat is greatly reduced to a few dots of the original (as has happened), do the incoming migrants from the rain forest simply get lost or are they able to locate these patches of relatively suitable habitat?

To view sphingid moths as moving back and forth across tropical Costa Rica, just as birds move back and forth between North American forests and those of Latin America, brings to mind other processes involved with migration, processes we are just beginning to understand. The sphingids, for example, are major pollinators of vines, shrubs, epiphytes, and treelets in both rain and dry forests. How would the elimination of either end of the migratory route, or the part in between, affect these plants?

How representative are sphingids of all the other insects that could be making the migratory trip? W. A. Haber tells us that the butterflies make complex movements back and forth over the same passes that the sphingids move through at night. There are massive movements of tachinid flies out of Santa Rosa's dry forests about the same time that the sphingids leave, in the middle of the rainy season. And F. G. Stiles tells us that Costa Rican birds move up and down the mountains with the seasons.

The implications of all this for conservation should be obvious. A tropical dry forest national park clearly does not and can not exist unto itself. It must exist in consort with the rain forest vegetation that is the recipient of the migrants. Likewise, a rain forest national park may well need a dry forest to which to airmail some of its populations for rejuvenation. The flyway between must also be conserved, placing a premium on dry forest parks that join directly to rain forest. As a case in point, Santa Rosa National Park is well isolated from rain forest, but its proposed expansion into Guanacaste National Park—eight times as large as Santa Rosa—not only joins Santa Rosa to the rain forest to the east but even includes some of the rain forest habitat that is the recipient and generator of Santa Rosa's migrant sphingids and other animals.

A country's or region's national parks form an organism that is greater than the sum of their individual areas and species. Conservation planning thus becomes more complicated; but far better to deal with the complications now than "discover" decades hence that species loss from a national park could have been avoided through regional planning. ●

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