

The Deflowering of Central America

*Because its species are highly specialized and intricately interrelated,
a tropical ecosystem under human assault quickly collapses*

by Daniel H. Janzen

"Did you hear about the fantastic bat netting at the COMELCO ranch? We caught twenty-one species in four hours."

"Well, you could have done that right out back five years ago."

"What would you get now?"

"Maybe five, maybe seven."

I overheard this conversation between three biologists who were conducting bat longevity studies at Finca La Pacifica, a ranch in the prime cattle-raising and cropland region of Guanacaste Province in Costa Rica. Two of them had just returned from banding bats at COMELCO, a larger, corporation-owned ranch, thirty-five miles away, and the site of one of the two remaining remnants of relatively large, undisturbed lowland deciduous forest from Guatemala to the Panama Canal Zone. (The other, also in Guanacaste, is in the Parque Nacional Santa Rosa.)

The COMELCO tract is now in the process of being cut and bulldozed in order to create more pastureland for the approximately 100,000 head of cattle that roam wild there. Five years from now, some biologist might repeat the last half of that conversation, but he will probably be studying bats at

COMELCO instead of at Finca La Pacifica.

Examples of the local or total extinction of Central American species through habitat destruction are recounted ad nauseum by those studying the animals and plants in these vaporizing habitats. For example, in 1965 I collected thirty-two species of wild bees, totaling about 1,500 individuals, from the flowers of an *Andira* tree (known locally as carne asado) in Guanacaste Province; in 1969 I collected four species, totaling twenty-three individuals, from the same tree at the same time of year. In 1965, at the same site, I dispatched two howler monkeys that had been crippled by a car while crossing the Pan American highway; today there are no more howler monkey road-kills in this area—the forest habitat of the howler has been destroyed for miles back from the highway.

What escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions. Many of the remaining participants of these interactions will probably hold on for many years, but they constitute little more than a haphazard, semi-self-sustaining zoo and botanical garden. Their complex behaviors, morphologies, and physiologies seem unnecessarily complex, even maladaptive, in the defaunated fence-row-pasture-field habitats they now occupy. And I use the word "occupy" advisedly; for example, many tree species, represented by mature individuals left when the forest was cut, exist only by virtue of their longevity.

The extinction of an interaction

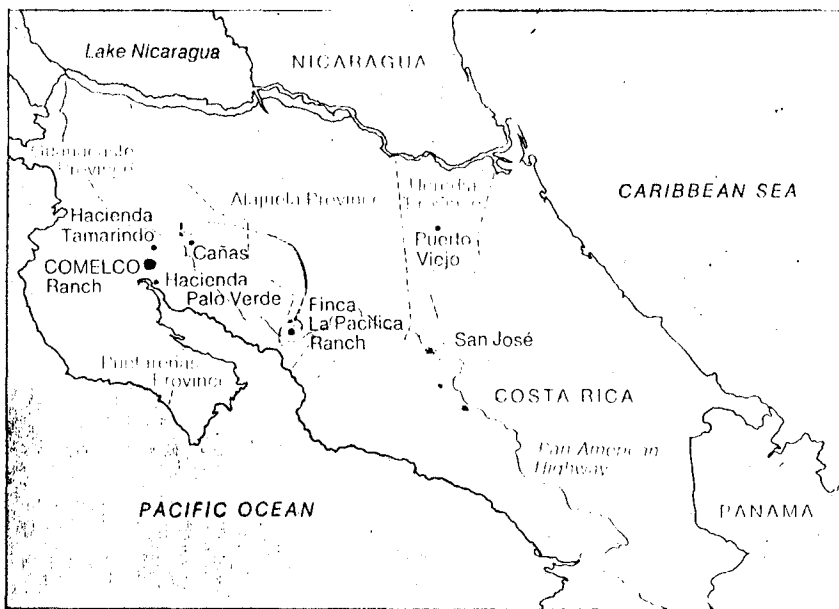
system occurs in many ways, but there is one consistent characteristic: the animals and plants involved no longer interact in the manner that originally led to selection for the production and maintenance of the traits they now display.

An esoteric, yet in many ways representative, example illustrates this point. During the dry season (January to the end of April) of 1970, I collected about 7,000 seed pods from about twenty-five guaiacal trees (*Hymenaea courbaril*, Leguminosae), most of which were growing in fence-rows, open pastures, and river-edge forest, and along roadsides. Remnants of a once extensive forest, the trees were generally fifty or more years old. In approximately 50 percent of the pods collected, the seeds had been infested by the larvae of a large weevil, *Rhynchonellus stigma*.

This weevil has one important characteristic: When the larva is mature, it excavates a cavity almost, but not all the way, through the very hard pod wall and then pupates inside the pod. The adult weevil hatches about the time the pod falls from the tree, completes the cut through the pod wall, and then disperses into the habitat.

I collected the pods directly below the guaiacal trees and gave little thought to the meager evidence of dispersal agents below the tree, such as rodents that chew into the pods or deer that break open the pods with their feet. Such animals would be the principal means by which the heavy pods and seeds could be scattered to new growing locations.

Foraging male Eulaema topica bees visit a Catasetum orchid in Oaxaca, Mexico. The flowers are fertilized through an exchange of pollen, which adheres to the bees.



However, 18 of the 7,000 pods contained another species of a closely related, but undescribed, *Rhinochenus*. The larvae of this weevil pupated without first cutting an exit hole through the hard pod wall, and in all but one of the 18 pods, the newly hatched adult weevils had died of starvation. My past experiences with seed predators had led me to believe that they are not likely to exist at such a low density. Since the adult weevils of this species did not have the behavior appropriate for escape from the pod, I speculated that this was probably an example of an incorrect host. But my search for an alternate host was fruitless; in Guanacaste Province there are no other trees with pods even vaguely resembling those of the guapinol.

Then while browsing in the British Museum of Natural History's Central American weevil collections made by George C. Champion at the turn of the century, I found that he had collected many of the now rare *Rhinochenus* at one of my collection sites, but had found only a few *R. stigma*. Champion was a careful collector with a reputation for accurate labeling. Obviously many changes have occurred in the six decades since Champion did his collecting; for one thing, the population of large terrestrial rodents, primarily agoutis and pacas, had been all but eliminated by hunting and habitat destruction.

I was left with the speculation that large rodents had to open the pods for adults of the rare *Rhinochenus* to escape. This hypothesis is substantiated by the observation that when a pod containing this weevil is opened, the adults run rapidly away from the pod in all directions; an adaptive item of behavior because pacas and agoutis are insect- as well as seed-eaters.

To test this idea further, I searched out several guapinol trees growing in small tracts of forest where agoutis and pacas were still present. In samples of these seed pods the "rare" *Rhinochenus* was by far the more common species and *R. stigma* was extremely rare. It thus appears that in areas where agoutis and pacas are heavily hunted or their habitat destroyed, the currently rare, undescribed *Rhinochenus* is still present only by virtue of occasional immigrant females flying in from remnant bits of semi-intact forest. In the forest, however, it outcompetes *R. stigma* to such a degree as to completely reverse their relative abundances. In short, over most of the guapinol population in Guanacaste Province, the undescribed *Rhinochenus* is extinct because of the elimination of large rodents. We can predict that *R. stigma* will disappear next, as the old remaining adult guapinol trees are thinned out by lumbering to the point where they are too far apart for the weevils to fly easily

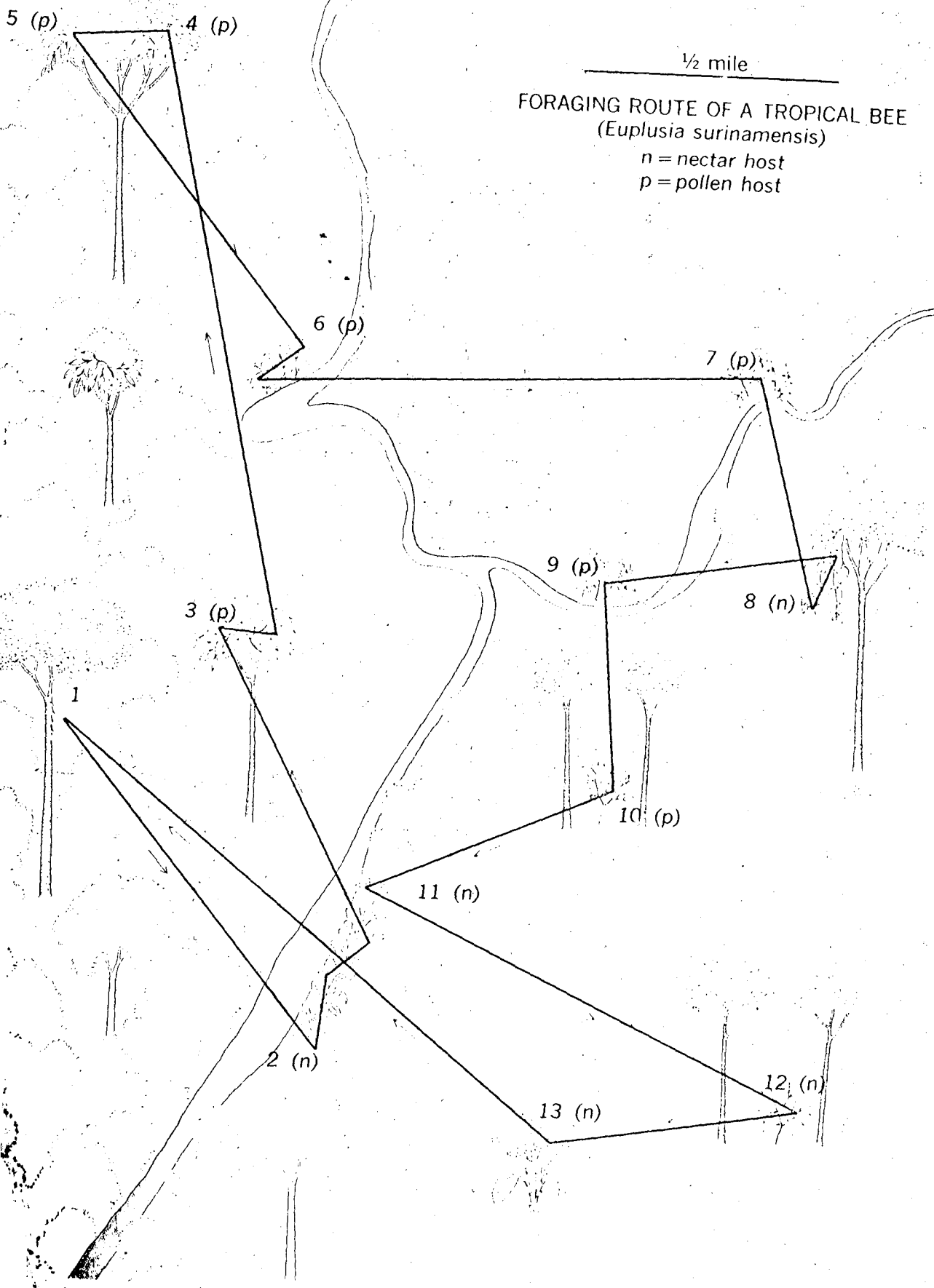
from one seed crop to the next.

Future field ecologists may also be misled on an important aspect of guapinol physiology. Like many tropical tree species, a specific guapinol does not bear seeds every year. There is a considerable body of theory and evidence that suggests that this genetically determined behavior is an adaptive mechanism. For example, if the weevils that locate a particular guapinol produce enough larvae to destroy the seeds in, say, 200 pods, then a tree that produces only 200 pods each year will have no surviving seeds, but a tree that produces 400 pods every other year will have a 50 percent seed-survival rate in terms of seed predation by weevils.

When I first started keeping records on fruiting periodicity of the guapinol, most of the trees under observation were growing in pastures, fencerows, and roadsides. As expected, only one-third to one-fifth of the trees bore fruit in 1969, the first year of observation, suggesting that the trees had a three- to five-year interval between fruit crops. However, I discovered that some of the same trees again bore large pod crops in 1970, and a few even fruited again in 1971.

A consideration of the mechanism for fruiting leads to a possible solution. A normal guapinol tree growing in a forest is under severe lateral crown competition from ad-

In Costa Rica Euplusia surinamensis, a typical bee species, memorizes and flies this hypothetical foraging route, or trapline, to collect nectar and pollen from flowering plants. The nest (1) is constructed 130 feet above the ground under the loose bark of a tree. Ground plants (2, 11, 13), shrubs (6, 7, 9), understory trees (10, 12), vines (3, 5, 8), and an epiphytic shrub (4) are visited daily.



FORAGING ROUTE OF A TROPICAL BEE
(Euplusia surinamensis)

n = nectar host
 p = pollen host

1/2 mile

adjacent trees. The same applies to its roots. Therefore, only a small fraction of the total photosynthate (products of photosynthesis) produced each year can be stored for eventual sexual reproduction; the remainder is expended in maintenance metabolism. The tree contains a triggering mechanism that initiates fruit production in the year when its reserves have accumulated to the point of permitting maturation of a single large pod crop. The size of this crop and the time period between crops is determined by natural selection; the amount of gain in seed survival through waiting one more year is balanced against the loss in sapling production by not putting new seeds into the habitat each year.

This pattern continues until someone cuts down the neighboring, competing species that keep the sun from reaching all but a small part of the guapinol's crown. The crown then gets more laterally oriented sunlight, and the tree responds with greater leaf production. The seed-triggering mechanism is probably short circuited in the following manner: In the first sterile year after the last pod crop, the tree stores as much photosynthate as normally accrues only after two or three years in a forest. It then produces a seed crop and probably even accumulates enough reserves during that year for another full pod crop. Exceptionally isolated trees may be able to keep this up for three or four years, before becoming sterile for a year or two to build up reserves again.

Therefore, a guapinol tree deprived of its everyday interactions with neighboring trees is, ecologically, highly abnormal, and difficult to use as a model for understanding the coevolution of the tree and its seed predators. The situation is akin to attempting to understand the evolution of the foraging behavior of bears by watching them open garbage cans in a national park.

The tropics abound with other examples of the extinction of an ecological interaction. The stately *palma real* (*Scheelea rostrata*) in Guanacaste Province is worth noting. This palm was once abundant in swamp forests and on moister ad-

jacent hillsides through the lowland forest. Because its habitat makes outstanding pasture, the forest was cleared. Numerous adult palms were left standing, however, because they cast little shade on the grass and cattle chew the edible pulp off the nuts. One is led to believe that here is one tree that will survive human activities. Not so, for unless a rodent ventures far into the pasture and takes a seed into the forest, the palms in the pasture are stone dead as far as any future population is concerned. Their seeds fall, germinate, and grow into healthy seedlings during the rainy season; but when the dry season comes, they die of drought in soil that is fully exposed to the sun.

The destruction of interspecific interactions by human habitat exploitation is by no means restricted to those tropical areas where much of the land has been cleared for farming. The following example from the Costa Rican rain forest is only one of many that could be cited.

Traveling during the early hours of the morning along roadsides and trails near the old town of Puerto Viejo in Heredia Province, one occasionally sees large female bees visiting the flowers of low roadside shrubs. These individuals, of the species *Eulaema cingulata* and *Euplusia surinamensis*, are removing the pollen from the tubular anthers of, for example, *Cassia* (a legume) and *Solanum*, a plant in the potato family. These bees and plants are common inhabitants of weedy areas in the lowlands from southern Mexico to Panama.

If we could follow these bees about in contemporary, badly disturbed plant communities, we would find that they fly from their nests to clumps of flowering *Solanum*, *Cassia*, *Bixa*, and *Conostegia*, collect the pollen, and then return to the nest. We would see almost nothing to indicate the important role that they—and many other euglossine bees of the family Apidae—played in the primary forest from which the fields and pastures were cut.

In the primary forest, these long-lived bees were in great part responsible for outcrossing many spe-

cies of woody plants that occurred as widely scattered individuals in a very diverse forest. The general foraging pattern, as pieced together from circumstantial evidence in many Central American forests, was as follows: Each day the female bee left her nest and flew a well-memorized feeding route, visiting each of a long series of plants. These plants were often several hundred yards or more apart and the whole of her route covered as much as six to twelve miles. By marking and releasing bees at various distances from the nest, I have found that within an hour some of these bees return to the nest from as far as fourteen miles away. This could mean that they have outstanding homing abilities; it could also be that they had become familiar with this section of forest through memorization of many plant sites. Such familiarity is further suggested by the observation that some returned to the nest with a pollen load.

Each plant visited by these bees produces only one to a few new flowers each day, but flowering may go on for as much as six months. While the bee may have initially located the plant through a search pattern in which flower odor and appearance were important, on its daily visits it returns purely through memory of the site. This was easily determined when the bees returned to the plants after the flowers had been removed.

The basic importance of these bees is that they are reliable outcrossing agents for a large number of tropical plants that normally occur at very low population densities and that have often been thought of as inbreeders because of the great distance between reproductive adults.

However, the opportunity to study the bee's behavior and its effi-

This Costa Rican orchid of the genus Mormodes is an outcrosser, dependent upon bees for cross pollination.

iciency as an outcrosser is gone in early all lowland rain forest areas under moderate to heavy human influence. As the forest is broken up, nest-site destruction removes part of the bee population. Of more interest here, however, is that the rushy pastures provide large stands of some of the plants that once were widely scattered in the forest or on occasional natural disturbed sites along a river. The surviving bee species now condense their feeding routes to incorporate primarily these plants. Not surprisingly, it is only the more generalist and flexible bee species that can do this, and not surprisingly, these presently are the ones with the widest geographic distribution.

In short, we still see a few of the bees, but they are not doing what they were doing for centuries. We see some of the plants, and some of them are still reproducing by virtue of an occasional visit by an occasional bee. But we have no idea what effect the reduction of outcrossing will have on the population of the plants.

It is important to note that re-

duction of the population density of the plants from which these bees obtained food was probably responsible for the extinction of many of the more rigid (specialized) species of euglossine bees. To make a success of a feeding strategy that centers around a feeding route, there must be a large number of plants reliably present; the long flights between plants do not allow much time and energy for searching for new plants. As the habitat is simplified through lumbering, grazing domestic animals, the building of housing, and other human activities, there are bound to be certain areas where the plant species that the bee formerly relied on are absent. This creates a downward spiral. As a bee drops out, the pollination frequency for an array of plant species will decline and the resultant reduced reproductive rate may cause these plants to drop out of the community.

We have not yet touched on a major interaction that disappears when the euglossine bees and their pollen and nectar hosts drop out. Male euglossine bees are the famous

"orchid bees" of the New World tropics; many are highly host-specific pollinators of orchids. The natural absence of these bees from most Caribbean islands is probably responsible for the lack of many species of orchids on these islands. While large old trees left in pastures may be festooned with orchids, the pollinators are gone, and since most of these orchids appear to be obligate outcrossers, incapable of self-pollination, they too will eventually disappear. The males of orchid bees appear to travel extraordinary distances to find very isolated plants, but as rain forest destruction becomes widespread, this ability is of little consequence.

There is only one moral to these accounts. All that is green and trees is not a forest. Forests are not random collections of animal and plant species. For a plant or animal to be something other than what it is in a zoo, all of the elements of its ecosystem must be present. The number of still-surviving adults is no reliable measure of how close a particular species is to extinction □

