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Fruit Bats: Prime Movers of Tropical Seeds

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Tropical forests are notably dependent on fruit-eating birds and mammals for dispersal of their seeds. Indeed, it has been suggested that the spectacular evolutionary success of tropical flowering plants over the past 135 million years can be attributed to their reliance on animals for pollination and seed dispersal, rather than the wind. Seed dispersal by animals is advantageous in tropical habitats for at least three important reasons. First, it allows seeds and seedlings to escape from such natural enemies as invertebrate and vertebrate seed-eaters, herbivores, and fungal pathogens. Second, it reduces the competition seedlings would experience if they germinated at high densities around the parent plant. Finally, widespread dispersal by creatures as mobile as birds and mammals allows plants to colonize new habitats1.

Specialization

The fruits of pioneer plants, those that are first to populate cleared areas of forest, contain enormous quantities of small seeds which are usually eaten by a diverse group of fruit-eating birds and mammals. Except for these, tropical plants appear to have specialized on particular groups of animals for dissemination of their seeds. For example, Charles Janson2 reported that two-thirds of the 258 species of fruit he examined in a Peruvian moist tropical forest could be classified as "bird" or "mammal" fruits. Bird fruits were characterized as being relatively small, unprotected by a husk, and either red, black, white, blue, or purple in color. In contrast, mammal fruits were characterized as being large, often protected by a husk, and either orange, yellow, brown, or green in color. Mammal fruits can be further subdivided into primate and bat fruits, with the latter often occurring in the plant families to which figs and their relatives belong (Moraceae), the chicle family (Sapotaceae), myrtle (Myrtaceae), palm (Palmae), black pepper (Piperaceae), and tomato families (Solanaceae).

Two families of bats, the neotropical leaf or spear-nosed bats (Phyllostomidae) and the paleotropical flying foxes (Pteropodidae), each contain over 100 species of fruit-eaters responsible for dispersing seeds from hundreds of species of tropical trees and shrubs. Many of these bats also pollinate a broad variety of plants, including a large number that are commercially valuable. Bats of these two families are often among the most numerous of all tropical mammals in undisturbed tropical forests, where they are unpersecuted by man. By virtue of their abundance and highly mobile lifestyles, these animals play an essential role in the seed dispersal ecology of tropical forests.

Seba's Short-tailed Fruit Bat

Although fruit-eating bats have been known to science for over a century, their impact on the dynamics of tropical forests has been investigated only recently. The most intensive of these studies is one that several colleagues and I conducted between 1974 and 1984 on the behavioral ecology of Seba's Short-tailed Fruit Bat (*Carollia perspicillata*) in the tropical dry forest of Santa Rosa National Park, Costa Rica.

A leaf-nosed bat weighing a little over a half an ounce (19 grams), Seba's Short-tailed Fruit Bat probably is the most common bat in all of Latin America. It ranges from southern Mexico to northern Argentina and occurs in a variety of lowland tropical habitats. At Santa Rosa and elsewhere, it roosts in caves and hollow trees and shares its roosts with other phyllostomids, such as the Long-tongued Bat (*Glossophaga soricina*) and the Common Vampire (*Desmodus rotundus*).

Our work has shown that the social organization of bats of the genus *Carollia*, of which there are four species, strongly influences the foraging and seed dispersal behavior of individuals. Females roost during the day in small harem-like clusters that are strongly defended by single reproductive males. Fewer than 20% of all adult males in the roost have reproductive access to females; the other 80% are "bachelors" waiting their turn to gain access to a group of females. Reproductive males defend their "harems" day and night and must feed in the immediate vicinity of the roost. Most of the seeds they ingest cannot become established as seedlings since they are deposited within their day roost. The major seed dispersers, therefore, are females and bachelor males, who sometimes forage up to two to three miles from their roost at night.

Food selection

Because of its relatively small size, Seba's Short-tailed Fruit Bat is restricted to eating smaller fruits containing numerous small seeds. Although it occasionally eats fruit produced by some canopy trees of the fig family (such as *Chlorophora tinctoria*) and *Spondias mombin* (Anacardiaceae), the bulk of its diet comes from fruits produced by shrubs. The most favored are those of the genus *Piper*, from the black pepper family, and such early successional trees as *Cecropia peltata* of the fig family, and *Muntingia calabura* (Elaeocarpaceae). Because of their preference for *Piper* fruits, *Carollia* bats can be accurately described as *Piper*-eating bats. They are, in fact, the most important seed dispersers of this genus of plants containing hundreds of species in the neotropical region.

Different kinds of bats have diverse roles in the ecology of tropical forests, each genus of fruit or nectar-eating bat important to different groups of plants. *Carollia* is crucial to pioneer and early successional plant species, but not necessarily to more mature forest trees. For example, *Carollia* infrequently eats figs (*Ficus*), and hence is not an important factor in the dispersal ecology of this species-rich group of canopy trees. In contrast, some of its most common leaf-nosed relatives, bats of the genus *Artibeus*, do eat figs.

Factors that influence ö*Carollia's*ò choice of food, in addition to fruit and seed size, include nutritional characteristics of the fruit pulp and the seasonal pattern of fruit production. They avoid eating fruit with a pulp rich in fiber, such as figs, and preferentially eat fruit rich in protein and carbohydrate, such as *Piper*. Females are especially "picky" eaters and have higher energy demands than most males, mainly because they are either pregnant or lactating for 10 months of the year. *Carollia* also avoids plants whose fruits ripen largely all at once and hence are available for only a short time. Instead, they concentrate on plants that produce fruits for extended periods of time, a pattern that is characteristic of certain pioneer species, such as *Cecropia*.

Because of its food choices, Seba's Short-tailed Fruit Bat is a relatively sedentary bat at Santa Rosa. Although some individuals forage up to three miles from the day roost, most fly no more than a mile before beginning to feed. In a typical night, an individual will eat about 35 *Piper* fruit or 8-10 *Cecropia* fruit, and spend long periods of time eating and resting in two or three feeding areas. It will harvest one fruit at a time and take it less than 300 feet to a solitary night feeding roost, doing this two to four times in rapid succession,

and then resting quietly for a half hour or more while its meal digests. Small seeds quickly pass through its digestive tract and are defecated either under the night roost or in flight between there and its next food plant. Most seeds are thus dispersed relatively short distances from their parents; longer dispersal distances occur when bats change feeding areas and fly back to their day roost before dawn.

Replenishers of rain forests

Seba's Short-tailed Fruit Bat has several important effects on the reproductive success of its food plants. The bat is a very reliable visitor to fruiting plants and finds nearly all of the ripe fruits of *Pipers* and other species the first night they are available. As a result, most of the seeds of its food plants are removed from the immediate vicinity of their parent plants and escape the attention of seed-eating insects and rodents. In addition, seeds are separated from fruit pulp when they pass through the bat's gut and are excreted in a manner that reduces their vulnerability to destruction by fungus. Certain seed species (some *Cecropia*, but not *Piper*) actually have higher germination rates after they have passed through the guts of bats. Because of its abundance (cave roosts at Santa Rosa contain up to 400 Seba's Short-tailed Fruit Bats each), this bat and other frugivorous bats are responsible for dispersing enormous numbers of seeds throughout the forest each night.

In order to understand the importance of just this one species of fruit bat, consider that the seeds of fruits eaten in one night by a single Seba's Short-tailed Fruit Bat may number as high as 60,000. This quantity will vary according to the kind of fruit eaten, but probably averages in the tens of thousands. Even if each bat averaged only 1,000 seeds nightly, just one colony of 400 would disperse 146 million seeds annually. Most of these would be dropped in places where they could not immediately germinate or where they might be destroyed by seed predators. Nevertheless, even if only one tenth of one percent of the seeds were to germinate, 146,000 new seedlings would result each year from the seed rain produced by this colony. We estimate that each square meter of forest floor receives between 12 and 80 bat-dispersed seeds annually.

A number of studies of tropical forest succession conducted in both the New 3-6 and Old World 7,8, as well as our work at Santa Rosa, indicate that frugivorous bats play an extremely important role in the regeneration of forests in disturbed habitats. In the neotropics, bat-dispersed plants (such as *Cecropia, Piper, Muntingia, Solanum* and *Vismia*) are among the first and most abundant plants to invade natural and man-made clearings, either because their seeds were dormant in the soil in large numbers before the disturbance or because they were defecated in flight soon after the clearing was formed. Quick to grow and mature, these plants attract hungry bats which also may bring later successional plant species into the clearing in a process that leads to continued forest growth. A study of forest regeneration along Peruvian floodplains 9 concluded that dispersal either by the wind or by bats was the most effective way for fast-growing trees to colonize newly exposed soil. If either means of transport were eliminated, the diversity of new plants would be greatly reduced, in turn supporting fewer kinds of animals.

The impact of bat seed dispersal

Frugivorous bats play a vital role in the maintenance of species-rich tropical forests. Because of their unique lifestyles, defecating in flight while commuting between their day roosts and feeding grounds, bats are among the most effective long distance dispersers of tropical seeds. This is particularly true of Old World flying foxes (especially species of *Pteropus*) which can carry seeds many miles□ sometimes between islands in the southeast Pacific□ in their nightly foraging trips 10.

The specializations of fleshy-fruited plants and their vertebrate frugivores that we see in tropical forests today are the result of millions of years of evolutionary interplay. Because of these specializations, tropical plants will suffer reduced dispersal success and survival whenever their particular frugivores, be they bats, birds or primates, are persecuted by man. Although much of the Amazon basin is still heavily forested, its primate populations have been hunted nearly to extinction, as Princeton University ecologist, John Terbough, has noted. The loss of these mammals will drastically alter the population dynamics of monkey-dispersed trees.

Similarly, the large-scale destruction of populations of fruit-eating bats, during misguided campaigns to eradicate vampires, will adversely affect the reproductive success of their food plants. In the absence of fruit-eating bats, reforestation of cleared areas will become much more difficult. The long-term survival of some of Latin America's most valuable plants may be seriously jeopardized, and a significant number of tropical trees and shrubs will lose an important ally their exclusive seed dispersers.

(Bio)
Theodore H. Fleming is a Professor of Biology at the University of Miami in Coral Gables, Florida. Dr. Fleming has studied the ecology and behavior of tropical mammals in Panama and Costa Rica for over 20 years. His book, "The Short-tailed Fruit Bat: a Study in Plant-Animal Interactions", which summarizes the results of his ten-year study of Carollia Perspicillata *in Costa Rica, will be published in the spring of 1988. During the 1987-88 academic year, he will be a Fulbright Fellow at James Cook University in Queensland, Australia, where he will be studying the seed dispersal ecology of rain forest flying foxes.*

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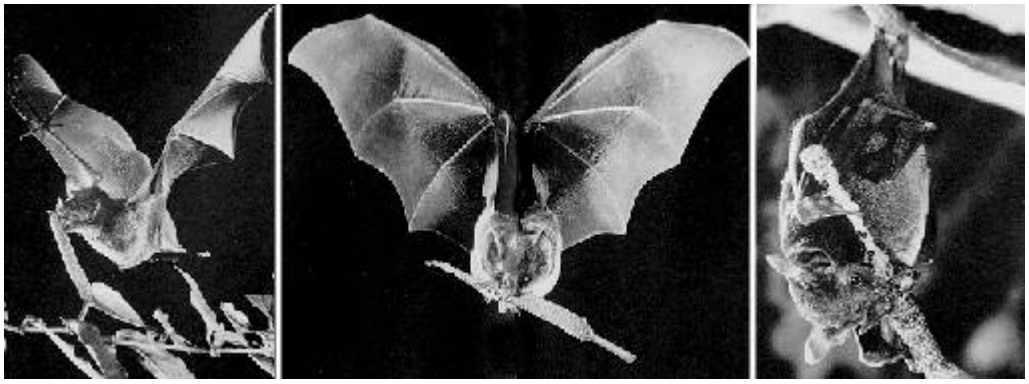
Seba's Short-tailed Fruit Bats cluster on the ceiling of Cendero Bat Cave in Santa Rosa National Park, Costa Rica. A typical colony of 400 may disperse up to 146 million seeds annually. PHOTO BY MERLIN D. TUTTLE



A Seba's Short-tailed Fruit Bat approaches a ripe Piper fruit, plucks it from the plant and flies to a nearby feeding roost. It may eat up to 35 of these fruits in a night, ingesting and dispersing thousands of seeds in the process. PHOTO BY MERLIN D. TUTTLE