VOLUME 9, NO. 4 Winter 1991

On Fruits, Seeds, and Bats
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by Donald W. Thomas

From the low hillock where I sat at the LAMTO Tropical Ecology Research Station in Ivory Coast, West Africa, the savanna appeared unusually sharp in the cool early-dawn air. The rich, green grassland, studded with tall *Borassus* palms and low shrubby trees, swept downslope to meet the tall, dense riparian forest bordering the Bandama River. Not far off to the left, a narrow strip of gallery forest wound its way through the savanna, following the moisture and fire protection offered by the depression of a seasonal stream. To my right, I could make out the more dense shrub and tree cover of the "savanne non-brulé," a patch of savanna that for the last 13 years had been protected from the annual fires and was now well on its way to becoming a true forest patch.

I had come to LAMTO to study fruit bats and their interactions with the trees and shrubs that make up this forest-savanna mosaic so typical of the moist savanna zones of West Africa. For over a year I had been setting my nine by 38-foot nylon "mist" nets to catch bats as they foraged in the different forest and savanna habitats that make up this part of West Africa.

From the seasonal fluctuations in the abundance of straw-colored flying foxes (*Eidolon* helvum) and collared fruit bats (*Myonycteris torquata*), I knew they were migrants, moving northward out of the coastal forest belt into the savanna zones at the start of the rainy season and retreating back to the forest, months later, as the rains ended. From recaptures of banded individuals, I also knew that other bats, such as Buettikofer's, dwarf epauleted, and Angola fruit bats (*Epomops buettikoferi, Micropteropus pusillus*, and *Lissonycteris angolensis*), were residents of the savanna throughout the year. By identifying the pollen and seeds that I found in the feces of bats as I netted them, I was also able to get a pretty good idea of who ate what, when, and where.

Now, sitting with the landscape laid out so clearly in front of me, I made a mental checklist of what I knew. The huge iroko tree (*Chlorophora excelsa*) standing well above the canopy of the gallery forest produced small sponge-like fruits that straw-colored flying foxes ate almost exclusively as they began their northward migration. And there beside it was a kapok tree *(Ceiba pentandra*), which produced flowers that opened at night, and which straw-colored flying foxes fed on as they returned south at the end of the rainy season.

On the edge of the gallery forest where the savanna abruptly ends, I could tick off a number of plants producing fruits commonly fed on by several species of fruit bats. The low fig trees *(Ficus capensis* and *Ficus vallis-choudae*) fruited throughout the year and were the staple diet for Buettikofer's and dwarf epauleted fruit bats. Epauleted bats also fed on wild relatives of the passion fruit (*Smeathmannia pubescens*), and two species of *Adenia* (*A. cissampeloides* and *A. miegei*) when they fruited in the rainy season.

Out on the savanna were numerous *Bridelia (B. ferruginea*), a tree producing small blue berries that were also used by straw-colored flying foxes as they retreated southward to the forest zone. There, where the savanna had been scalped by a bulldozer making a new access road, was a dense cluster of *Solanum* (*S. verbascifolium*), an African relative of the tomato, eaten only by collared and Angola fruit bats.

The trees colonizing the "savanne non-brulé" were dominated by cape figs (*Ficus capensis), Bridelia, Smeathmannia*, and several other trees and shrubs. They had at least one thing in common: they were all eaten by fruit bats. Scanning this landscape where so many of the trees and shrubs produced fruits sought after by bats, I pondered the complex relationship between tropical plants and fruit-eating animals.

Those of us raised in the temperate zone tend to think of forests as dominated by trees that produce small dry seeds, which either simply fall to the ground, or are scattered by the wind around the "mother" tree. This strategy obviously works well in the temperate zone where summers are relatively short and seed-eating insects don't have time to build up large populations between the unfavorable winter periods. However, it is a dangerous reproductive tactic in the tropics. When seeds fall in high density around the mother tree, seed-eating insects easily find them. In a hot and humid tropical climate, these seed predators rapidly build up large populations and few, if any, seeds survive long enough to germinate.

In the tropics, many plants have evolved an alternate reproductive strategy to circumvent this seed-predator problem. Here, 80-95% of the trees and shrubs hide their seeds inside an edible fruit. These fruits, often sweet and succulent, are the bait that trees use to attract a large variety of frugivorous bats, birds, monkeys, opossums, and even rodents.

During their feeding, these frugivores swallow small seeds and so disperse them in their feces great distances from the mother tree. When fruits are too large to be eaten rapidly, frugivores typically carry them off to distant trees where they can feed safely, thus dispersing even large seeds tens to hundreds of feet away. By dispersing seeds away from the mother tree, frugivores render at least two important services. First, they allow many seeds to escape certain death below, enhancing the tree's reproductive success. Second, they allow trees and shrubs to send out seeds to colonize sites that would otherwise not have been accessible to them. Tropical plants are caught up in an intimate relationship with fruit-eating animals and, without frugivores, plant communities would not be as we see them now.

So, where do fruit bats fit in the ecology of tropical forests and savannas? Looking over the savanna at LAMTO and noting that the trees and shrubs that bats commonly fed on were also among the most abundant, it was tempting for me to conclude right then that bats were a major factor in structuring this plant community. But to even begin to understand the role that the fruit bats play in structuring any tropical plant community, several questions must be answered. What proportion of fruit of a given species is eaten by fruit bats? Do fruit bats disperse the seeds to sites that this species typically colonizes? Are the seeds viable after passing through a bat's gut? Can these seeds escape seed predators long enough to germinate?

In search for answers to these questions, I designed a series of simple experiments that I conducted over several years. First, I focused on the cape fig, a tree species that commonly grew along the edge of the gallery forest and was one of the first "forest" trees to invade the savanna zones as soon as fires were reduced. The cape fig produces five to over 100 fruits every six weeks to several months throughout the year. Half the size of apples, these fruits could easily be eaten by monkeys, squirrels, birds, or bats.

Over a period of several months, I individually numbered 1,149 unripe fruits on 38 trees. By doing rounds at sunset and first light, I was able to determine when each fruit ripened, whether it fell or was eaten, and, if eaten, whether this happened during the day (suggesting birds, monkeys, or squirrels) or at night (bats). The results were striking. Most fruits disappeared within the first 24 hours after ripening, and a full 75% of fruits were removed during the night, presumably by bats.

Although fruit bats were the primary consumers of cape fig fruits, this did not necessarily mean that they were the frugivores responsible for the proliferation of cape fig trees in the unburned savanna. To test this, I set out hundreds of 10-foot-square plastic sheets along transects at two sites in the savanna near the forest edge and at one site in the unburned savanna. I avoided setting sheets under trees, so any feces deposited were likely from flying frugivores,

either birds or bats.

If fruit bats were effective seed dispersers, I reasoned that most seeds should appear during the night. Again, the results were astounding. Feces literally rained down on the collecting sheets, and bats accounted for over 92% of all this precipitation! When I considered only the feces containing seeds, bats were even more important; they accounted for over 95% of the seed-bearing feces at any site! Similarly, bats deposited 94 to 100% of the cape fig seeds I found on the various transects. Remembering that birds and other diurnal frugivores removed 25% of cape fig fruits, I was surprised to learn that they only accounted for 0 to 6% of the "seed rain."

Bats were obviously very good at translating fruit consumption into the dispersal of seeds to possible colonization sites. Although I did not know why at the time, a small experiment that I performed several years later in Costa Rica provided some answers. There, I found that birds stayed longer in trees when feeding and so "unloaded" more of their seed-bearing feces under the fruiting tree than did bats. Bats moved more of their ingested seeds away from sites where seed predation is typically high, thus behaving as "high quality" seed dispersers.

Fruit bats may well move large numbers of seeds, but are these seeds viable? If not, then all this prolific seed rain is but ecological noise and unimportant in determining the structure and dynamics of plant communities. To determine whether the seeds germinated, I took fruit bats and cape fig fruits into a large laboratory that, much to the chagrin of the station manager, I used as a flight cage.

Buettikofer's and dwarf epauleted fruit bats were amazing to watch feeding on the fruits. By confining these bats one at a time in the flight cage, and providing them with unlimited amounts of fruits, I showed that the little 18 to 32 gram dwarf epauleted fruit bat ate an astounding two times its body weight in fruit every night! The larger 160 to 200 gram Buettikofer's epauleted bat ate between 190 and 240 grams of fruits per night.

When feeding, the bats stuffed their mouths to bulging, then slowly and methodically chewed the mass, swallowing only the easily digested juices and many seeds. When finished, they spat out a compressed mass of fiber, including some seeds, which I called a rejecta pellet. During their frequent flights, they left the walls peppered with seed-filled fecal splotches, resembling those I found on the plastic collecting sheets in the savanna.

From these observations I could identify three categories of seeds: those that remained untouched in the fruit, those that had been masticated but spat out in the rejecta pellet, and those that had passed through the gut and showed up in the feces. To test the effect of the bats' treatment of the seeds, I collected hundreds of seeds from ripe fruits, rejecta pellets, and feces and placed them on moist blotting paper to germinate. Fecal seeds were the first to germinate. After only six days, more than 50% had sprouted, and it took only a few more days before all the seeds had germinated. Seeds from rejecta pellets took a little longer (14 days for 50% germination) and only 75% germinated. In contrast, no more than 10% of seeds I extracted from ripe fruits ever germinated--even after 89 days.

Passage through a bats' gut obviously had a highly beneficial affect on seeds, removing any germination inhibitors and leaving them viable and primed to germinate. However, the vast numbers of seeds that accumulated either in the rejecta pellets that bats dropped under their feeding trees, or in fruits that fell uneaten below cape fig trees, could still be the most important source of new seedlings if these were the seeds that best escaped predation by ants and other predators.

To see which seeds survived the best, I took bunches of fecal seeds and set them out on small plates, some alone and others in contact with a piece of fruit. Ants found all of these seeds quickly but found those associated with fruit first. In only 24 hours, ants removed 92% of the seeds with fruits, but in the same time they found only 72% of the seeds that were alone. In a contest against seed predators and time, fecal seeds would appear to be those most likely to survive long enough to give rise to the next generation of seedlings and trees.

The story that emerges from this study is that, from a plant's perspective, fruit bats are extremely good frugivores. They eat enormous quantities of fruits each night and disperse prodigious numbers of seeds across the savannas.

These fecal seeds escape seed predators better than others and are primed by their travel through a bat's gut to germinate as soon as conditions are appropriate.

It would seem that my first instincts were correct. Fruit bats do indeed play a singularly important role in dispersing seeds, not just of the cape fig, but of many of the most common trees and shrubs in the West African forest-savanna mosaic. Now when I speak to school groups, I describe fruit bats as farmers of the tropics, sowing seeds and determining which trees will grow when openings become available.

Worldwide, there are some 250 species of fruit bats* that nightly either pollinate the flowers or disperse the seeds of well over 500 species of tropical trees and shrubs in the Americas, Africa, Asia, Australia, and Oceania. This is the largest group of mammalian frugivores, and we should not underestimate their importance both to tropical plant communities, and to us. Here are three examples to consider.

In West Africa, straw-colored flying foxes form colonies numbering upwards of a million individuals in the coastal forest belt during the dry season. Nightly, each quarter-pound bat eats and disperses the seeds of nearly half a pound of fruits of forest trees, many of which are economically important. Indeed, straw-colored flying foxes are the only animals known to disperse seeds of the iroko tree whose timber has a commercial value in the millions of dollars annually. In one night, a single colony may disperse the seeds of nearly a half million pounds of iroko and other fruits throughout the surrounding forest. With the onset of the rains, these colonies subdivide and begin an annual migration that takes them nearly 1,000 miles northward through the forest, savanna, and sahel regions, eating and dispersing seeds along the way. I am awestruck when I think of just how important these bats must be in ensuring the successful dispersal of seeds over such a vast area!

In South America and Asia, indiscriminant logging and slash and burn agriculture leave vast areas of forest denuded, dry, and prone to erosion each year. Regeneration of these sites progresses first by invasion of low, wind-dispersed plants and then by colonization of fruiting, animal-dispersed trees and shrubs. Establishing this latter tree and shrub stage is crucial to any subsequent forest development because it provides the shade, coolness, and increased moisture that the forest trees require for germination and growth. By dispersing the seeds of pioneering trees and shrubs like the cape fig into these areas, fruit bats play a key role in reclaiming these lands. Unfortunately, in Central and South America beneficial fruit bats are often the victims of indiscriminate blasting of caves to control vampire bats [*BATS*, Spring 1991].

On many islands in the Indo-Pacific Oceans, the large, colonial flying foxes are the only vertebrate pollinators and seed dispersers present. Here, these bats fill all the roles normally occupied by flower-visiting sunbirds, hummingbirds, and sugar-gliders and by fruit-eating birds, monkeys, opossums, and rodents elsewhere in the tropics. There is good reason to believe that elimination of these bats would have a catastrophic impact on island forests. For many trees, reproduction and seed dispersal would simply cease.

Yet, it is exactly on these islands where hunting for the luxury food market has posed the most serious threat to fruit bats. Overhunting and inter-island trafficking of fruit bats has already led to the extinction of several species and has caused severe reductions in the populations of others. We can only hope that the various island countries will fully support a strict ban on commercial hunting of fruit bats and so ensure the continued integrity of these fragile island ecosystems. International trade is now illegal, a ban imposed by the CITES treaty in late 1989 [*BATS*, Winter 1989-90], but treaty nations must also enforce it [*BATS*, Fall 1990].

So, the next time you take an evening walk and feel a drop of something wet on the back of your neck, just think; if this were the tropics, that could be some bat's way of ensuring a plant's reproductive success!

[bio]
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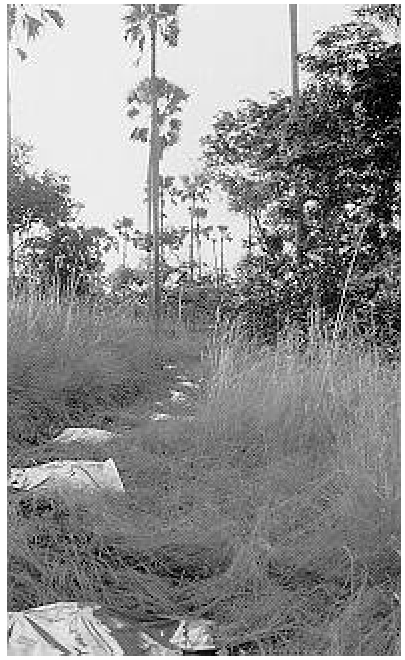
dearly regrets having left the tropics.

[footnote]
**The general term "fruit bats" actually refers to species in two families, the spear-nosed bats (Phyllostomidae) of the Americas and the Old World fruit bats (Pteropodidae), also referred to as flying foxes, of Africa, Asia, Australia, and the islands of the Indo-Pacific Oceans.*

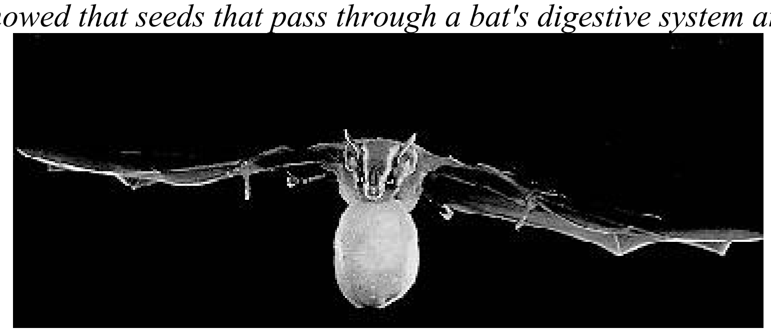
Above: Cape figs, one of the trees that dominate the West African savanna, are a staple diet for dwarf epauleted fruit bats. As year-round residents of the savanna, these bats are one of the cape fig's most important seed dispersers.

The annual migrations of straw-colored flying foxes take them nearly 1,000 miles across much of Africa. Huge colonies of these bats, sometimes numbering over a million individuals, can disperse the seeds of up to a half million pounds of fruit every night along the way.



In the author's study, plastic sheets serve as seed collectors. He discovered that bats accounted for over 95% of the "seed rain" in any given study site.

When feeding, this Buettikofer's fruit bat stuffs its mouth to bulging, slowly chewing the fruit and swallowing many seeds. The author's study showed that seeds that pass through a bat's digestive system are the first to germinate.



By carrying large fruits away from the "mother tree," fruit bats enhance the reproductive success of many plants throughout the world's tropics, dispersing even large seeds great distances. In Latin America, this tent-making bat (Uroderma bilobatum) carries a fig almost as big as he is.

Throughout the Old and New World, regeneration of forest clearings begins with "pioneer" plants. In this rain forest clearing in French Guiana, South America, bat seed-dispersed plants were the first to appear. These photos, taken over a two and a half year period, show the progression from barren land to lush growth. Nearly all woody plants seen are bat-dependent.

All articles in this issue: