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## Fruits and Bats: Supply and Demand in the Tropical Rainforest

By

Elisabeth K. V. KALKO\*

Plant-animal interactions play pivotal roles in tropical forests. Pollination, seed dispersal, and herbivory are regarded as fundamental factors contributing to the establishment and maintenance of the high species diversity in the tropics, particularly in tropical lowland forests. We are focussing in our research on the role of bats (Chiroptera) with a particular emphasis on fruit-eating bats as seed dispersers. On one hand we ask what kind and how many fruits are offered by plants to fruit-eating bats and how the fruits are presented to their „customers“ for a goal-directed and easy find. On the other hand, we study what bats need from fruits and what kind of services they deliver in return to the plants.

Interactions of fruit-eating bats and plants have lead to a wide range of mutual adaptations. Availability and access to fruits as resources have a major impact on the organization of bat assemblages over space and time, influencing their foraging behaviour, namely use of space as well as refinement of sensory systems and morphology to find and successfully harvest ripe fruits (e.g., KALKO 1998, KALKO & HANDLEY 2001, KALKO & al. 1996a). Bats as major seed dispersers affect phenology patterns of plants and contribute to the formation of fruit syndromes including specific ripening patterns and nutritional content of the fruits (e.g., KORINE & al. 2000, THIES & KALKO 2004, WENDELN & al. 2000).

In long-term studies on Barro Colorado Island (BCI), a field station of the Smithsonian Tropical Research Institute (STRI) in Panama (<http://www.stri.org>) we are focussing on two key stone plant resources that form the core diet of many fruit-eating bats, species of the genus *Ficus* (*Mor-*

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\*) Prof. Dr. Elisabeth K. V. KALKO, Institute of Experimental Ecology of Animals, University of Ulm, Albert-Einstein Allee 11, D-89069 Ulm, Germany, Europe & Smithsonian Tropical Research Institute, Balboa, Panama; e-mail: [Elisabeth.Kalko@uni-ulm.de](mailto:Elisabeth.Kalko@uni-ulm.de)

*aceae*) in the canopy and pepper plants, *Piper* sp. (*Piperaceae*), in the understory (see GIANNINI & KALKO 2004).

BCI harbours an astounding number and variety of bat species. Up to now, more than 70 species have been registered on the 15.6 km<sup>2</sup> island. About 20 species classify as frugivores, ten of which make up the bulk of all captures (> 80 %) in our community-based studies (KALKO & al. 1996b), underlining their important contribution as seed dispersers. With an estimated population of around 10,000 individuals on BCI alone, fruit-eating bats are likely to move millions of fruits every year (KALKO 1997). All fruit-eating bats in the Neotropics belong to the endemic family of New World leaf-nosed bats (*Phyllostomidae*). The high number of fruit-eating bats and the composition of their diet which consists in most cases almost exclusively of fruit ensure a high reliability as dispersers over time (GIANNINI & KALKO 2004, KALKO 1998).

Seed dispersal by fruit-eating bats is highly beneficial to the plants. To better understand this aspect we will be describing the basic features of this process. With few exceptions (KALKO & CONDON 1998), bats detect ripe fruit mostly by scent (KORINE & KALKO 2005, THIES & al. 1998). This makes sense as fruits are often hidden between leaves and hard to detect otherwise in the dark. The species of both key taxa, *Ficus* and *Piper* that are mainly dispersed by bats produce distinct odour plumes when ripe, undoubtedly to attract their dispersers.

After detection of a possible food source, the bats approach a shrub in the understory or a tree crown in the canopy and repeatedly circle around the fruits (KORINE & KALKO 2005, THIES & al. 1998). They continuously emit echolocation signals to orient in space and to assess the exact position of the fruits. After an individual bat has selected a ripe fruit, it approaches it in a goal directed flight (Fig. 1) and grasps it with its mouth, often accompanied by a brief landing. The fruit is then brought by the bat in flight to a temporary dining roost which is usually within 100–200 m or sometimes less of the fruiting tree or shrub. There the bat immediately processes the fruit (Fig. 2) by masticating the fruit tissue, mostly without damaging the seeds. The fruit tissue is then squeezed out by pressing it with the strong tongue against the ridged palate (KALKO & al. 1996b). The fruit juice is ingested and the dry pellets of the remaining fruit tissue are spat out. Accumulations of dry pellets in the forest are indicative of a temporary dining roost of a bat. Overall, small seeds are swallowed whole with the fruit juice and excreted later, either at a roost or in flight. Large seeds are dropped at the dining roost.

As the bats do not eat the fruits in the trees or shrubs where they have picked it up, probably because of a higher predator pressure in the trees lurking for prey, the plants benefit from the transportation of the seeds away from the parent plant. Furthermore, as most dining roosts are in small



Fig. 1. The common fruit bat (*Artibeus jamaicensis*) approaching a ripe fig in flight. - Photo credits: Dietmar NILL.



Fig. 2. The common fruit bat (*Artibeus jamaicensis*) feeding on a ripe fig. - Photo credits: Dietmar NILL.

openings within the vegetation, seeds have a high chance to reach suitable germination sites. With one exception, none of the phyllostomid bats is known as seed predator by chewing seeds. Cleaning the fruit tissue off from larger seeds when processing the fruit as well as the subsequent gut passage for small seeds are likely to further enhance germination success.

Given the highly efficient and effective dispersal process, many plants have invested in the presentation and nutritional content of their fruits with respect to dispersal by bats. Our studies have shown tight links of fruit characteristics and phenology for both focus groups, *Ficus* and *Piper* (KALKO & al. 1996b, KORINE & al. 2000, THIES & KALKO 2004). Free-standing figs (formerly subg. *Pharmacosyce*) and strangler figs (formerly subg. *Urostigma*) alike offer huge fruit crops with several thousands to several ten thousands of fig fruits (syconia) per tree. As figs fruit asynchronously over the year on the individual as well as on the population level due to their peculiar pollination biology with highly specialized, minute wasps, they provide frugivores with a continuous, aseasonal fruit supply.

Several fruit characteristics foster detection by bats and permit resource partitioning. Figs that are primarily dispersed by bats remain green(ish) with no distinct change in colour (KALKO & al. 1996b, KORINE & KALKO 2005, KORINE & al. 2000). They ripen synchronously, offering only fruit for about 4–7 nights. Green-fruited figs broadcast a distinct, species-specific odour plume when ripe. This olfactory signal is enhanced by the synchronous mass ripening of the fruit over a few nights. The majority of the green-fruited figs is removed at night (60–90 % of fruit crop). The proportion of fallen fruit is mostly less than 1 %, underlining the high contribution of nocturnal frugivores to the dispersal process. Furthermore, green-fruited figs come in a wide range of sizes (1–30 g), thus fostering intricate resource partitioning among fruit-eating bats with larger bats feeding mostly on large figs and smaller bats feeding on smaller figs (KALKO & al. 1996b, WENDELN & al. 2000).

In contrast, figs that are mainly dispersed during the day (60–74 % of fruit crop) turn red when ripe and ripen asynchronously over several weeks, sometimes even months (KORINE & al. 2000). Their main consumers are visually orienting birds. Furthermore, red-fruited figs do not appear to produce strong odours and their fruits are all rather small (1–2 g), facilitating gulping by birds.

Nutritional analysis has shown that figs contain a broad range of different proteins and lipids in the fruit tissue in addition to large amounts of water-soluble and complex carbohydrates (see WENDELN & al. 2000). Most importantly, some figs, namely free-standing figs such as *F. insipida*, are characterized by a high content of calcium, a mineral crucial for reproduction of mammals such as bats (KALKO 1998). It appears that figs are more than just „cheap“ abundant and sweet fruits in the forest. Our stu-

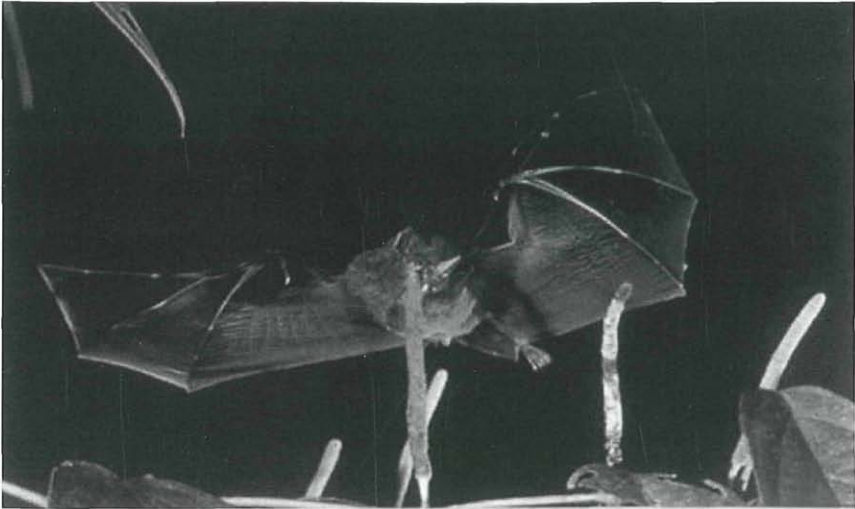


Fig. 3. The short-tailed fruit-bat (*Carollia castanea*) approaching a spike of a ripe pepper plant (*Piper* sp.). – Photo credit: Dietmar NILL.

dies on BCI are currently focussing on shedding more light into the role of figs as keystone resources.

We also found very tight links on BCI between bats and Pepper plants (*Piperaceae*) (THIES & KALKO 2004, THIES & al. 1998). In the neotropics, the genus *Piper* is composed of two distinct functional groups with several species each: gap *Piper* that grows under rather high light conditions in forest gaps and at forest borders and forest *Piper* that is adapted to low light conditions of the understory in the tropical rainforest. Both groups differ in phenology with respect to their main dispersers. Gap *Piper* is dispersed on BCI by a wide range of frugivores, including birds with removal rates of ~4 % over a five week period, ants with ~26 % and bats with ~49 %. The rest usually falls off. Fruit availability is about one fruit spike per plant and day. Most gap *Piper* species fruit several times per year. 95 % of the fruits started to ripen in the morning at about 6 pm, probably as an adaptation to the diurnal dispersers.

This pattern contrasts strongly with forest *Piper*. There, individual species fruit only once per year in a distinct rhythm that leads to a low but continuous overall availability of fruits throughout the year. Some species fruit almost a year after they have flowered synchronously with other forest *Piper* species in the dry season. This in addition with a peculiar ripening pattern where fruits only start to become soft and fragrant in late afternoon after 3:30 pm strongly suggests a tight relationship with bat dispersal. This was confirmed by our studies where we found that almost 90 % of the fruits of forest *Piper* are removed by bats.

Several species of bats, namely short-tailed fruit bats (*Carollia* sp., Phyllostomidae) are highly specialised on *Piper* as core diet (THIES 1998, THIES & KALKO 2004). Behavioral preference test with two species, *C. perspicillata* and *C. castanea*, support the assumption of different degrees of specialization with regard to *Piper* fruits (THIES 1998). Whereas *C. perspicillata* is more generalistic in its food choice and feeds on several types of fruits including a few species of *Piper*, *C. castanea* (Fig. 3) is highly specialised and feeds almost exclusively on *Piper*, including a wide range of species. The differences in food preference are accompanied by distinct differences in foraging strategy where the smaller species, *C. castanea* uses smaller home ranges and only one foraging area per night in contrast to *C. perspicillata* that roams over larger distances and uses several foraging areas per night. Those behavioural differences contribute to differential contributions of both *Carollia* species with regard to seed dispersal and they also underline factors that promote co-existence and hence diversity of ecologically similar bat species.

A detailed analysis of the spatial and temporal use of night roosts by *C. castanea* where several animals were radiotracked over a several year period brought new insights into their effectiveness as seed disperser (THIES 1998, THIES & al. 2007). Contrary to expectations based on literature reports on other frugivorous bats, *C. castanea* did not repeatedly return to the same night roost night after night. To the contrary, each night roost was re-visited only about 1.5 times. This means that the seed shadow created by *C. castanea* is scattered and not clumped as it has been hypothesized for bats before. Low re-visitation rates of night roosts ensure broad dispersal of seeds even when the bats themselves use only small home ranges. Thus, fruit-eating bats do not only serve as „taxi“ for seed transportation but their feeding behaviour enhances chances for successful germination and establishment further because of their high mobility and dynamic in roost selection and use.

Other interesting examples for the contribution of bats for seed dispersal can be found in the foraging behaviour of tent-making bats. These comprise of small phyllostomid bats that roost in self-made „homes“, where they modify large leaves of plants into shelters against rain and predators (WILCKEN & KALKO 2004). Presumably, tent-making bats follow fruit-resources, profiting from the relatively easy set-up of leaf-tents as temporary roosts. Recent studies have shown that these species are highly mobile despite their small size and are able to maintain stable populations even in severely fragmented habitats provided the distance between the fragments is not too large and that the fragments still contain sufficient resources (ALBRECHT & al. 2007).

To summarize, intricate interactions between bats and plants in the species-rich tropics facilitate co-existence and foster diversity not only

among but also between both groups, leading to a multitude of mutual adaptations including morphological, physiological and behavioural aspects.

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