

## Fruit Bats (Chiroptera: Pteropodidae) as Seed Dispersers and Pollinators in a Lowland Malaysian Rain Forest<sup>1</sup>

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### ABSTRACT

The aims of this study were to (1) characterize the food resources exploited by fruit bats (Pteropodidae) within an old-growth Malaysian dipterocarp forest, (2) test the viability of the seeds they disperse, and (3) provide an estimate of the proportion of trees that are to some degree dependent upon bats for seed dispersal and/or pollination. Fruit species exploited by bats could be distinguished from those eaten by birds largely on the basis of color (as perceived by human beings). Bat-dispersed fruits were typically inconspicuous shades of green–yellow or dull red–brown, whereas fruits eaten by birds were generally bright orange to red. Dietary overlap between bats and nonflying mammals was relatively high. In contrast to primates and squirrels, which were major seed predators for several of the plant species under investigation, fruit bats had no negative impact on seed viability. A botanical survey in 1 ha of old-growth forest revealed that 13.7 percent of trees ( $\geq 15$  cm girth at breast height) were at least partially dependent upon fruit bats for pollination and/or seed dispersal.

*Key words:* bats; dispersal; frugivory; Malaysia; nectarivory; pollination; syndromes.

FRUIT BATS SHARE A LONG EVOLUTIONARY HISTORY with many of their food plants and as important seed dispersers have had a major influence upon the selection of fruit traits and the diversification of the angiosperms throughout the tropics (van der Pijl 1957, Fleming 1979, Marshall 1983). Hence, the fruits of many tropical plant species share morphological features that reflect the sensory capabilities of bats. These morphological features, which include drab color, strong odor, and exposed positioning, were used by van der Pijl (1957) to describe what is known as the “bat-dispersal syndrome,” as perceived by human beings. The distinct morphology of these fruits was believed to reflect both the importance of bats as seed dispersers and the relatively low levels of dietary overlap between bats and other major frugivore groups (van der Pijl 1957, Fleming 1979).

Subsequent research, however, has revealed the bat-dispersal syndrome to be more variable than initially believed (Heithaus 1982, Kalko *et al.*

1996). In particular, several authors have drawn attention to differences in the dispersal syndrome between New World phyllostomid and Old World pteropodid fruit-eating bats (Heithaus 1982, Kalko *et al.* 1996).

Phyllostomid and pteropodid bats are believed to have been geographically separated throughout their adaptive radiation (Fleming 1979, Heithaus 1982). Whereas phyllostomid bats are restricted to tropical and subtropical regions of the Americas, pteropodid bats are distributed widely throughout many tropical and subtropical regions of Africa, Asia, and the Pacific. Hence, the fruit characters of Neo- and Palaeotropical bat-dispersed plants are believed to have evolved independently in both hemispheres (Fleming 1979, Heithaus 1982). Thus, it has been argued that differences in the bat-dispersal syndrome between each of these geographical regions may reflect (1) the contrasting flight and sensory capabilities of small echolocating phyllostomids and their generally larger non-echolocating pteropodid counterparts (Kalko *et al.* 1996) and (2) different levels of dietary overlap between bats and other major seed-dispersing frugivore groups

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in Neo- and Palaeotropical forests (Fleming *et al.* 1987).

Bat-dispersed fruits of the Neotropics are morphologically distinct from those dispersed by birds, and can often be differentiated by humans largely on the basis of color and odor (Fleming 1988, Gorchoff *et al.* 1995, Kalko *et al.* 1996). Phyllostomid bats generally consume dull green fruits, some of which produce strong odors when ripe (Fleming 1988, Kalko *et al.* 1996). In contrast, fruits consumed by birds are primarily odorless and are produced in shades of red, purple, and blue (Snow 1971, Janson 1983, Wheelwright *et al.* 1984, Fleming 1988, Gorchoff *et al.* 1995, Kalko *et al.* 1996, Korine *et al.* 2000). The occurrence of these two distinct dispersal syndromes is thought to reflect both the importance of olfaction in food location by phyllostomid bats (Thies *et al.* 1998) and the low levels of dietary overlap between these two major frugivore groups (Fleming 1979, Fleming *et al.* 1987, Gorchoff *et al.* 1995, Kalko *et al.* 1996, Korine *et al.* 2000).

In contrast, the bat-dispersal syndrome in the Palaeotropics is morphologically variable and can include fruits of several different colors (including reds, purples, greens, and blues), some of which are strongly scented when ripe (van der Pijl 1957; Thomas 1982; Marshall 1983; Gautier-Hion *et al.* 1985; Phua & Corlett 1989; Richards 1990; Utzurrum 1995; Eby 1998; Tan *et al.* 1998, 1999). Palaeotropical examples also commonly include species with specialized modes of presentation, whereby fruits are produced directly from the bole of the tree (caulicarp), directly from main leafless branches (ramicarp), or at the end of long pendulous stalks (flagellicarp). Although the importance of olfaction in food location has been demonstrated with captive pteropodids (Acharya *et al.* 1998), the bright color and exposed positioning of many bat-dispersed Palaeotropical fruits may reflect (1) the relative importance of visual cues for food location by pteropodid bats (Kalko *et al.* 1996), (2) the low maneuverability of many large species of pteropodid, and (3) the large amount of dietary overlap between pteropodid bats and other major seed-dispersing frugivore groups within the region (Fleming *et al.* 1987).

In some cases, however, the bat-dispersal syndrome in the Palaeotropics may be quite distinct (Gautier-Hion *et al.* 1985; Phua & Corlett 1989; Richards 1990; Utzurrum 1995; Tan *et al.* 1998, 1999). For example, Utzurrum (1995) has suggested that small pteropodid species (<50 g) in the Philippines appear to discriminate between fruits

largely on the basis of color, and generally consume dull, predominantly green fruits. Large species, in contrast, select fruits mainly on the basis of plant height and the available crop density per tree (Utzurrum 1995). This therefore suggests that the diets of large pteropodids may be diffuse and overlap with those of other frugivore groups, whereas the diets of smaller forest-dwelling species may be more distinct, like those of Neotropical phyllostomids. If the diets of small pteropodids are distinct, then this has important implications for conservation biology within the region, since any factor that may cause a decline in the abundance and diversity of fruit bats will also have serious implications for the reproductive biology of their food plants (Utzurrum 1995). The aims of this study were to (1) characterize the food resources exploited by pteropodid bats within an old-growth Malaysian dipterocarp forest, (2) test the viability of the seeds they disperse, and (3) provide an estimate of the proportion of trees within the forest that are to some degree dependent upon fruit bats for seed dispersal and/or pollination.

## METHODS AND METHODS

**STUDY SITE.**—This study was conducted at Kuala Lompat (3°43'N, 102°17'E), within the Krau Wildlife Reserve, Pahang, Peninsular Malaysia, between May 1997 and November 1999. The Krau Wildlife Reserve consists of a large area of old-growth forest (Clark 1996), which ranges in elevation from 50 m at Kuala Lompat to over 2000 m at the summit of Gunung Benom. The vegetation at Kuala Lompat can be classified as lowland evergreen mixed dipterocarp forest. Because it is relatively poor in dipterocarps and unusually rich in large Leguminosae, the site is not characteristic of most dipterocarp forest sites within the area (Raemaekers *et al.* 1980).

Although the study site has previously been described in detail by Raemaekers *et al.* (1980), the area surrounding the reserve has undergone considerable changes in recent years. At the time of the present study, the forest at Kuala Lompat bordered directly onto gardens and plantations, without a buffer zone (Fig. 1).

**THE FRUIT BAT ASSEMBLAGE AND THEIR FOOD PLANTS.**—The forest fruit bat assemblage at Kuala Lompat consists of nine species, three of which have long-term resident populations (*Balionycteris maculata*, *Chironax melanocephalus*, and *Cynopterus brachyotis*) and six of which are relatively transient

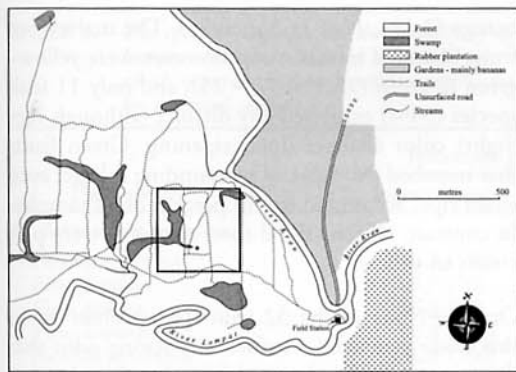


FIGURE 1. Map of the study site at Kuala Lompat, Malaysia. The position of the 1 ha vegetation plot was selected at random from within the 16 ha forest block outlined in bold.

(*Cynopterus horsfieldi*, *Dyacopterus spadiceus*, *Eonycteris spelaea*, *Megaerops ecaudatus*, *Megaerops wetmorei*, and *Rousettus amplexicaudatus*; Hodgkison 2001). Collectively, these bats feed on the flowers and/or fruits of at least 33 plant species that grow either within or directly adjacent to the old-growth forest (Hodgkison 2001). The observations and experiments described in this study were based on these food plant species (Appendix).

**CHARACTERISTICS OF FRUIT BAT FOOD RESOURCES.**—Descriptions of 33 known and 3 suspected (but unconfirmed) food plants were recorded from living specimens observed in the field. For each species of fruit and flower, notes were made on color, odor, and mode of presentation (*i.e.*, caulicarp, ramicarp, and flagellicarp/flory), along with a description of the plant growth form (*i.e.*, tree, liana, epiphyte, or strangler). It should be noted, however, that all descriptions of fruits and flowers were based solely on human rather than pteropodid perceptions of color and odor.

The feeding activity of other animal visitors was recorded from both nocturnal and diurnal field observations, and supplemented by data available in the literature. Detailed studies on primate diets (Chivers 1980) and *Ficus* fruit consumption by birds at Kuala Lompat (Lambert 1987, 1989; Lambert & Marshall 1991) were particularly valuable to investigate the degree of dietary overlap between bats and other fruit-eating vertebrate taxa.

**SEED GERMINATION.**—The viability of small seeds ingested by fruit bats during feeding was tested by germination trials using seeds freshly separated

from the pulp of ripe fruits as controls. Ingested seed samples used in these trials were obtained from fruit bat feces. Seeds from fresh feces were collected from four fruit bat species captured in mist nets within the study area (*B. maculata*, *Chironax melanocephalus*, *Cynopterus brachyotis*, and *D. spadiceus*; see Hodgkison *et al.* 2002 for mist-netting techniques). Captured individuals of two species (*B. maculata* and *D. spadiceus*) were also fed ripe fruits and held briefly in cloth bags until the seeds had been excreted. Collecting trays placed beneath the roosts of *B. maculata* provided an additional source of seed specimens, which had been excreted up to one month prior to their use in germination trials.

Seeds were arranged on moistened filter paper and placed in covered petri dishes for germination (Lieberman *et al.* 1979). All trials were conducted in the field in partial shade and under natural conditions of temperature and day length (*i.e.*, 22–32°C and *ca* 12 hours of daylight). Samples were inspected at regular intervals of one to three days for signs of germination using a hand lens, until several successive inspections revealed no further germination. A seed was considered to have germinated upon the first appearance of the radicle. In the case of two monoecious *Ficus* species, which were consumed by *D. spadiceus* (*i.e.*, *F. annulata* and *F. depressa*), germination trials were conducted using only entire seeds, thus excluding all seeds that had been parasitized by developing agoonid wasp larvae (Janzen 1979); however, since several bat species ingest a greater proportion of viable *Ficus* seeds than is found within the fruit (Janzen 1978, Uzzurum & Heideman 1991), the relative frequency of entire seeds present within both ripe fruits and *D. spadiceus* feces was measured by inspecting samples of each with a hand lens. Parasitized seeds were easily recognized by conspicuous holes in the seed coat, which were created by the adult wasps upon emergence.

The percentage of seeds that germinated within each trial provided the main measure by which the effect of ingestion was evaluated. The effect of ingestion upon the speed of germination, however, was also investigated in the case of four species that were used in feeding trials, since both the control and ingested seed samples were obtained from the same plants and sown simultaneously under identical conditions.

The final germination frequencies of each trial were arranged into 2 x 2 contingency tables (fresh vs. ingested x germinated vs. not germinated) and when possible were analyzed using a *G*-test of in-

