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Fruit Bats (Chiroptera: Pteropodidae) as Seed Dispersers and Pollinators in a Lowland Malaysian Rain Forest¹

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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 (≥ 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, Gorchoy *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 in shades of red, purple, and blue (Snow 1971, Janson 1983, Wheelwright *et al.* 1984, Fleming 1988, Gorchoy *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, Gorchoy *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

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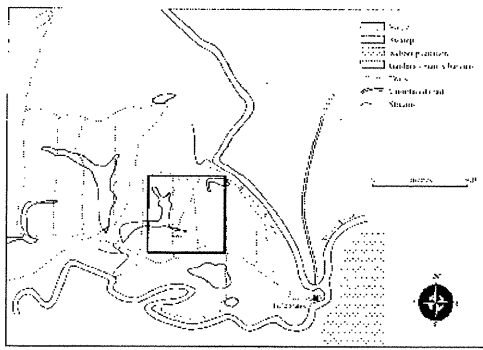


FIGURE 1. Map of the study site at Kuala Lompat, Malaysia. The position of the 1 ha vegetation plot was selected at random from within the 16 ha forest block outlined in bold.

(*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 agaonid 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, Utzurrum & 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-

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dependence (Sokal & Rohlf 1995). The effect of ingestion upon the speed of germination (*i.e.*, number of days) was analyzed by calculating the mean number of days from sowing to germination. Germination times within each of the trials were then compared using a Kolmogorov–Smirnov two-sample test (Lieberman & Lieberman 1986, Sokal & Rohlf 1995). When the identity of any defecated seed sample was uncertain, the developing seedlings were transferred into pots and grown in soil until they could be positively identified.

Large seeds that were not ingested by fruit bats during feeding were obtained from below feeding perches, day roosts, and from captured individuals that were given fruits to eat while held captive in cloth bags for periods of approximately half an hour. To assess the possible impact that fruit bats may have on the viability of these seeds, samples were inspected visually for signs of damage, particularly to the seed coat. Fruit bats were judged to have had no significant negative impact on seed viability if the seed coat was undamaged after feeding.

RELATIVE ABUNDANCE OF BAT-DISPERSED AND POLLINATED PLANTS.—A 1 ha vegetation plot was established to estimate the abundance of bat-dispersed and pollinated trees relative to other species within the forest (Condit 1998). The position of the plot was selected at random from within a 16 ha block of forest (Fig. 1). The survey included all trees with a girth at breast height (GBH) of equal or greater than 15 cm. Tree species (≥ 15 cm GBH) dispersed and/or pollinated by bats were marked with numbered aluminum tags. All other trees were marked with a small slash to the bark. Because a reliable minimum estimate was judged preferable to an overestimate of unknown error, the sample of bat-dispersed and pollinated plants included only reproductively mature specimens. Immature specimens, which are often difficult to recognize in the field, were classified as “other species” (*i.e.* they were not recorded as “bat plants”). Hence, this method inevitably underestimated the abundance of bat-dispersed and pollinated plants within the forest plot.

RESULTS

CHARACTERISTICS OF FRUIT BAT FOOD RESOURCES: COLOR.—The pteropodid bat community at Kuala Lompat consumed fruits in a variety of different colors, including deep red (6.25%, $N = 2$), brown (6.25%, $N = 2$), purple (6.25%, $N = 2$), and

orange (3.1%, $N = 1$; Appendix). The majority of fruits observed in this study, however, were yellow–green to green (78.1%, $N = 25$), and only 11 fruit species (34%) exhibited any distinct (although very slight) color changes upon ripening. Green fruits that matched the color of surrounding foliage, even when ripe, accounted for 50 percent of all samples. In contrast, all four floral food resources were pale cream to yellow.

ODOR.—None of the 32 fruit species observed in this study produced a sufficiently strong odor that the trees could be detected by a human observer within the field (Appendix). A few species (*e.g.*, *Ficus annulata*), however, did produce an odor that could be detected when the fruits were held close to the nose or when they had been sealed within a polyethylene bag.

In contrast, the flowers of *Parkia* and *Palaquium* spp. produced strong odors that could easily be detected within the forest. Nevertheless, the floral odors produced by each genus were markedly different. Whereas the scent of *Parkia* flowers was relatively sweet and pleasant, the odor of *Palaquium* flowers was distinctly sour and unappealing.

PRESENTATION.—Some plant species had adaptations that resulted in the fruits and/or flowers being held well away from the clutter of surrounding vegetation. Four species (11.1%) were caulicarpic and produced fruits directly from the trunk (*i.e.*, *Polyalthia* sp., *Ficus fistulosa*, *Ficus hispida*, and *Ficus scortechinii*). Two species (5.6%) were ramicarpic, and produced fruits directly from leafless main branches (*i.e.*, *Cyathocalyx scortechinii* and *Garcinia parvifolia*). Four other species (11.1%) were flagellilcarpic or flagellifloric and produced fruits and/or flowers on the end of long downward-pointing peduncles (*i.e.*, *Fagraea racemosa*, *Prunus polystachya*, *Parkia javanica*, and *Parkia speciosa*).

OTHER ANIMAL VISITORS.—Primates, civets, and squirrels consumed at least 20 (55.6%) of the 36 known or suspected fruit bat food resources under investigation (Appendix). Since observations were incidental rather than systematic, this figure can only be regarded as a minimum estimate. In several cases, primates and squirrels were major seed predators and consumed the seeds of at least three species of fruit (9.4%) prior to their ripening. In contrast, dietary overlap between bats and birds was low and included only two species of fruit (5.6%).

SEED VIABILITY: SMALL SEEDS.—Twelve (37.5%) of the 32 fruit species observed in this study con-

assemblage

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TABLE 1. *The effect of ingestion on the viability of small seeds dispersed by four species of fruit bat (A–D) at Kuala Lompat, Malaysia. Statistics refer to G-tests of independence (Sokal & Rohlf 1995). NS indicates species for which ingestion had no significant effect. Asterisks indicate that the ungerminated seed sample was too small for statistical analysis.*

Plant species	Percentage germination (<i>N</i>)		<i>G</i> _{adj.}	<i>P</i>
	Ingested seeds	Fresh seeds		
A. <i>Balionycteris maculata</i>				
<i>Fagraea racemosa</i>	56.3 (190)	60.0 (100)	0.36	>0.05 (NS)
<i>Ficus fistulosa</i>	95.7 (70)	100 (100)	*	*
<i>Ficus globosa</i>	86.2 (58)	NA	NA	NA
<i>Ficus scortechinii</i>	90.9 (460)	91.8 (500)	0.26	>0.05 (NS)
<i>Nauclea officinalis</i>	56.5 (200)	58.0 (100)	0.06	>0.05 (NS)
<i>Pellacalyx saccardianus</i>	86.6 (224)	NA	NA	NA
<i>Pterandra echinata</i>	56.7 (300)	59.5 (200)	0.39	>0.05 (NS)
B. <i>Chironax melanocephalus</i>				
<i>Ficus scortechinii</i>	100.0 (25)	91.8 (500)	*	*
C. <i>Cynopterus brachyotis</i>				
<i>Ficus fistulosa</i>	96.0 (100)	100 (100)	*	*
D. <i>Dyacopterus spadiceus</i>				
<i>Ficus annulata</i>	86.0 (150)	83.3 (150)	0.41	>0.05 (NS)
<i>Ficus depressa</i>	92.0 (100)	93.0 (100)	0.07	>0.05 (NS)

tained small seeds that were ingested by fruit bats during feeding. Fruit bats had no significant influence on the viability of small seeds when they were swallowed during feeding (Table 1). In the case of *F. annulata* and *F. depressa*, the proportion of whole seeds, as opposed to those parasitized by agaonid wasp larvae, was markedly greater in the feces of *D. spadiceus* (100%, *N* = 150; 100%, *N* = 100, respectively) than it was within the ripe fruits of the figs upon which they were fed (9.2%, *N* = 500; 7.6%, *N* = 300). These results therefore indicate that *D. spadiceus* selectively ingests fruit pulp that contains viable seeds.

Ingestion of small seeds by fruit bats had a statistical, although probably not an ecological, significant influence on the germination times of two

of the four species fed to *B. maculata* and *D. spadiceus* in feeding trials (Table 2). In the case of *F. racemosa*, ingested seeds took on average one day longer to germinate compared to seeds extracted from the pulp of ripe fruits. The ingested seeds of *F. depressa* germinated on average one day earlier than the control (Table 2).

LARGE SEEDS.—Twenty fruits (62.2%) contained seeds that were too large to be ingested by fruit bats during feeding. These seeds were either retained and scraped or dropped immediately by fruit bats during fruit handling (Appendix). Seeds that were retained and scraped were generally associated with hard fruits with thin pericarps, which often adhered tightly to the seed coat. These seeds were

TABLE 2. *The effect of ingestion on the germination times of small seeds dispersed by two species of fruit bat (A and B) at Kuala Lompat, Malaysia. Statistics refer to Kolmogorov–Smirnov two-sample tests (Sokal & Rohlf 1995). NS indicates species for which ingestion had no significant effect (*P* > 0.05).*

Plant species	Mean days to germinate (<i>N</i>)		<i>D</i>	<i>P</i>
	Ingested seeds	Fresh seeds		
A. <i>Balionycteris maculata</i>				
<i>Fagraea racemosa</i>	15 (190)	14 (100)	0.27	<0.01
<i>Ficus scortechinii</i>	11 (200)	12 (200)	0.12	NS
B. <i>Dyacopterus spadiceus</i>				
<i>Ficus annulata</i>	3 (150)	3 (150)	0.01	NS
<i>Ficus depressa</i>	3 (100)	4 (100)	0.38	<0.001

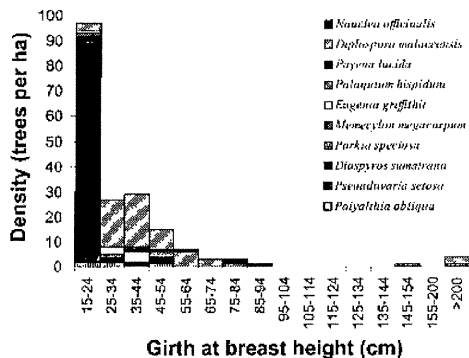


FIGURE 2. Density and species composition of fruit bat food plants in relation to girth size in a 1 ha plot of old-growth rain forest at Kuala Lumpur, Malaysia.

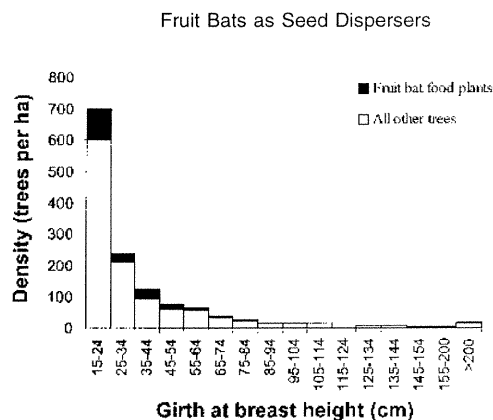


FIGURE 3. Relative density of fruit bat food plant in relation to girth size in a 1 ha plot of old-growth rain forest at Kuala Lumpur, Malaysia.

protected from physical damage by thick and sometimes very hard and woody seed coats. Seeds that were dropped immediately by fruit bats during feeding were generally associated with soft fruits in which the seed separated cleanly from the pulp. The seeds of soft fruits were often slippery and popped out of the fruit as soon as the pericarp was split open.

RELATIVE ABUNDANCE OF BAT-DISPersed AND POLLINATED PLANTS.—Ten of the 33 food plant species under investigation were identified within the 1 ha forest plot (Fig. 2). These plants ranged in size from small understory trees (15 cm GBH) to giant forest emergents (>200 cm GBH). Together these bat-dispersed and pollinated tree species represented 13.7 percent of a total 1368 trees sampled within the 1 ha forest plot (Fig. 3); however, since the “bat plant” sample included only reproductively mature tree specimens (≥ 15 cm GBH), this figure is likely a conservative estimate for the area sampled. The survey also excluded lianas and strangler figs (Appendix) as well as species that were unconfirmed as fruit bat food plants (*i.e.*, *Polyalthia* sp., *G. parvifolia*, and *Ochanostachys amentacea*).

DISCUSSION

DIETARY OVERLAP AND DISPERSAL SYNDROMES.—Dietary overlap between bats and birds was low, and food resources exploited by each could be largely distinguished on the basis of color as perceived by human beings. This was best illustrated by figs (*Ficus* spp.; Table 3). A total of 40 species of fig have so far been recorded within the study area at Kuala

Lompat (Lambert 1987, 1989; Lambert & Marshall 1991; present study). Despite extensive systematic studies, however, the ripe fruits of only one species (*F. sundaica*) have so far been recorded within the diets of both bats and birds (Table 3). In contrast to bird figs, which are mainly brightly colored (particularly shades of orange to red), species of fig eaten by bats were predominantly yellow to green and included four of the five caulicarpic species recorded in the study area. In contrast to bat figs of the Neotropics (Kalko *et al.* 1996), however, none of the *Ficus* species consumed by bats at Kuala Lumpur produced a strong odor that could be easily detected by humans.

Interestingly, the bright red fruits of four *Ficus* species that were consumed by large pteropodids (>100 g) in a montane forest in the Philippines (Utzurum 1995) were eaten by birds and/or rejected by small fruit bats (<100 g) in both localities (*i.e.*, the Philippines and Malaysia). This therefore suggests that the diet of large pteropodids may be relatively generalized; however, since many large pteropodid species often forage over vast areas of forest, it is likely that their choice of food will be more sensitive to the effects of habitat loss and environmental degradation on a landscape level than many smaller species, which are often closely associated with small forest fragments (Utzurum 1995). Since optimal foraging theory predicts that dietary niches are broader in areas of low biological diversity (Pianka 1981), it is likely that both large and small pteropodids will show greater dietary overlap with birds as a result of habitat loss and environmental degradation. Thus, when discussing dispersal syndromes, it is also important to consider

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TABLE 3. *Ficus* species at Kuala Lompat and their dispersal agents. Nomenclature follows Corner (1965).

<i>Ficus</i> species	Growth form	Fruit color	Dispersal agents			
			^a Brds	Bats	Pmts	Cvts
Subgenus <i>Urostigma</i> (monoecious)						
<i>F. annulata</i> Bl.	St	yellow-green		X	X	X
<i>F. benjamina</i> L.	St	pink-purple	X			
<i>F. binnendykii</i> Miq.	St	pink-purple	X			
<i>F. bracteata</i> Wall. ex King	St	red	X			
<i>F. caulocarpa</i> Miq.	St	pink-yellow	X			
<i>F. consociata</i> Bl. (var. <i>murtoni</i> King)	St	red-deep red	X			
<i>F. crassiramea</i> Miq.	St	red-deep red	X			
<i>F. cucurbitina</i> King	St	deep red-black	X			
<i>F. delosyce</i> Corner	St	pink-yellow green	X			
<i>F. depressa</i> Bl.	St	yellow-green		X		
<i>F. drupacea</i> Thunb.	St	deep red-purple	X			
<i>F. dubia</i> Wall. Ex King	St	deep red-purple	X			
<i>F. kerkhovenii</i> Val.	St	orange red-red	X			
<i>F. globosa</i> Bl.	L	yellow-green		X		
<i>F. magnoleaefolia</i> Bl.	T	yellow-green		X	X	
<i>F. pellucido-punctata</i> Griff.	St	purple	X			
<i>F. piscarpa</i> Bl.	St	yellow-orange	X			
<i>F. stricta</i> Miq.	St	red	X			
<i>F. stupenda</i> Miq.	St	red-deep red	X			
<i>F. subcordata</i> Bl.	St	red	X			
<i>F. sumatrana</i> Miq.	St	dull pink-ochre	X			
<i>F. sundaica</i> Bl.	St	orange-deep red	X	X		
<i>F. virens</i> Ait. (var. <i>glabella</i> [Bl.] Corner)	St	greenish ochre	X			
Subgenus <i>Ficus</i> (dioecious)						
<i>F. awantiacea</i> Griff.	L	black	X			?
<i>F. fistulosa</i> Reinw. ex Blum*	ST	yellow-green		X		
<i>F. grossularoides</i> (var. <i>robusta</i> [Burm. f.] Corner)	ST	dull orange				
<i>F. heteropleura</i> Bl.	St	red	X			
<i>F. hispida</i> Linn. F.*	ST	yellow-green		X		
<i>F. obscura</i> Bl. (var. <i>borneensis</i> [Miq.] Corner)	St	red-deep red	X			
<i>F. parietalis</i> Bl.	St	red	X			
<i>F. punctata</i> Thunb.	L	deep purple			?	?
<i>F. recurva</i> Bl.	St	red	X			
<i>F. sagittata</i> Vahl.	St	red-deep red	X			
<i>F. trichocarpa</i> Bl.	St	deep red	X			
<i>F. schwarzii</i> Koord.	ST	brown				?
<i>F. scortechinii</i> King	ST	deep red		X		?
<i>F. sinuata</i> Thunb.	St	red	X			
<i>F. subulata</i> Bl.	St	red	X			
<i>F. variegata</i> Bl.	T	green-pink		^a X		?

Key: *Ficus* species (* = species found only in secondary scrub outside of the forest); growth form (St = strangler/scrambler; ST = small tree; T = tree; L = liana); fruit color (ripe fruits); dispersal agents (brds = birds; bats = pteropodid bats; pmts = primates; cvts = civets; X = observed; ? = suspected).

^a Data from Lambert (1987, 1989) and Lambert and Marshall (1991).

both the size and the biological diversity of a habitat, particularly in relation to the home range of the species concerned.

Dietary overlap between bats and nonflying mammals was relatively high. But in contrast to bats, primates and squirrels were significant seed predators for a number of the plant species under investigation (Appendix). Bats also contrasted with nonflying mammals in relation to other important

aspects of their feeding behavior. Whereas primates and other nonflying mammals frequently remain in fruit trees while feeding (Corlett 1998), small pteropodids often carry fruits away to feeding perches before consumption (Phua & Corlett 1989, Utzurrum 1995, Hodgkison 2001). Hence, in some cases, a greater proportion of the seed handled by fruit bats may be carried away from the vicinity of the parent plant.

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SEED DISPERSAL.—Seed rain patterns and dispersal distances generated by small fruit bats are likely to depend primarily on seed size. Because large seeds are discarded by fruit bats during feeding, these seeds are only transported as far as the feeding perch before being dropped to the ground. The distance a bat may travel to reach a feeding perch is likely to depend on many factors, but can range from a few meters to 0.25 km (Phua & Corlett 1989, Bhat 1994, Funakoshi & Zubaid 1997, Marimuthu *et al.* 1998, Hodgkison *et al.* ~~in press~~); however, because individual bats often use the same feeding perch repeatedly, this perch can sometimes provide a focal point for the accumulation of large piles of seeds and rejected fruit parts. Hence, the food handling behavior of small fruit bats is likely to result in a restricted and often clumped pattern of dispersal for large seeds.

egested

2003

Small seeds that are ingested by fruit bats during feeding have the potential to be dispersed much farther, but, the distance over which these seeds are carried is likely to depend on how long they remain in the gut and how far the bat travels before defecating. Since fruit bats have short guts and a large intake of food, passage times are generally very rapid for all species (Phua & Corlett 1989, Uzzurum & Heideman 1991, Shilton *et al.* 1999, Hodgkison 2001). As a result, most seeds are ~~excreted~~ within *ca* 20 minutes to one hour after consumption. The distance a bat may travel within this time will depend upon several factors but ultimately will relate to the ranging behavior of the species concerned. Large, wide-ranging species such as *D. spadiceus* (Hodgkison 2001) are more likely to cover long distances and hence transport seeds farther than small species with relatively restricted ranges such as *B. maculata* (Hodgkison *et al.* ~~in press~~). Greater dispersal distances could be achieved with longer seed retention times. Shilton *et al.* (1999) demonstrated that small captive pteropodids can retain viable *Ficus* seeds in their guts for more than 12 hours during the day when they are not feeding; however, because these bats were inactive during this period (Shilton *et al.* 1999), the importance of this result to the long-distance dispersal of seeds is unclear. Nevertheless, the recolonization of the volcanic Krakatau islands by figs and other bat-dispersed taxa clearly demonstrates the importance of fruit bats for the long-distance dispersal of seeds (Whittaker & Jones 1994, Thornton *et al.* 1996, Shilton *et al.* 1999). Although fruit trees and feeding perches may still provide activity foci for most of the seed rain because many fruit bat species defecate during flight, the overall seed shadows are

likely to be relatively extended and more homogeneous compared to those produced for large, uningested seeds (Thomas 1982, Fleming 1988, Uzzurum 1995).

DISPERSAL QUALITY.—Due to the differential handling of large and small seeds, the dispersal service provided by fruit bats is likely to benefit different seed types in different ways. The seeds of pioneers, typically small and produced in large quantities within a single fruit, are generally adapted for invading and colonizing environments, which in natural forest ecosystems are unpredictable in both space and time (Swaine & Whitmore 1988). Hence, the wide and relatively homogeneous dispersal of small seeds by fruit bats is likely to benefit these plant species by increasing the chances of some seeds reaching a gap, either directly upon dispersal or from the soil seed bank when a gap is newly formed. The tendency of *D. spadiceus* to fly above the forest canopy (Hodgkison 2001) may also benefit the dispersal of strangler figs (*e.g.*, *F. annulata* and *F. depressa*), as these seeds may have a greater chance of being intercepted by vegetation than they would if dispersed by a more terrestrial animal such as a civet.

The seeds of non-pioneer species, which are typically large and produced in small quantities per fruit, are generally adapted for germinating within shade (Swaine & Whitmore 1988). The high nutrient content of these seeds may make them particularly attractive as a food resource for seed predators (Harper *et al.* 1970), especially within the high density aggregations found below fruiting trees (Janzen 1970). Although fruit bats generally disperse large seeds over relatively short distances, these small movements may still be sufficient to increase seed survival by reducing the probability of seed predation (Janzen 1970, Connell 1971) and by reducing intraspecific competition, both among the seedlings themselves and between seedlings and parent plants.

Fruit bats may further influence the probability of seed survival by the number and density of seeds they deposit in a single location. For example, the selective ingestion of viable *Ficus* seeds by *D. spadiceus* and other pteropodid species (Uzzurum & Heideman 1991, Uzzurum 1995) and the repeated use of feeding perches may actually increase the density of viable seeds deposited in a single location. Whether this treatment will be beneficial to the reproductive success of a plant will depend on many factors and is beyond the scope of the present study (Howe & Smallwood 1982).

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What is certain, however, is that fruit bats are important seed dispersers and pollinators for a major proportion of rain forest plants. Although there is still much to be learned about bat-plant interactions in Palaeotropical forests, even a conservative estimate suggests that 13.7 percent of trees (≥ 15 cm GBH) are at least partially dependent upon fruit bats for seed dispersal and/or pollination within a 1 ha plot of old-growth dipterocarp forest at Kuala Lompat, Malaysia. This figure is likely to increase as our knowledge of bat-plant interactions grows. Therefore, any decline in the abundance and diversity of fruit bats within these forests could have serious implications for the reproductive biology of a large proportion of rain forest plants.

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APPENDIX Continued.

Family	Species	Growth form	Color ^a	Odor ^a	Seed fate	Other consumers			
						Birds	Primates	Civets	Squirrels
Flowers									
Leguminosae	<i>Parkia javanica</i> (Lamk.) Merr.	T	Yellow and white	Y			N ^a		N
	<i>P. speciosa</i> Hassk.	T	Yellow and white	Y			N ^a		
Sapotaceae	<i>Palaquium hispidum</i> Lam	T	Cream	Y					N
	<i>P. obovatum</i> (Griffith) Engler	T	Cream	Y					N

Key: Growth form (St = strangler; ST = small tree; T = tree; L = liana); odor (Y = yes; N = no); seed fate (I = ingested; D = dropped; S = scraped); other consumers (F = fruit pulp; N = nectar and pollen; S = seeds; ? = may consume fruit pulp).

^a Data based on human perceptions of color and odor.

^b Data from Chivers (1980).

^c Data from Lambert (1987, 1989).

^d Taxonomy follows Leenhouts (1972).

^e Unconfirmed as fruit bat food plants.