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Feeding ecology of Philippine fruit bats: patterns of resource use and seed dispersal

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Synopsis

Information on diet composition of, feeding patterns in, and seed dispersal by pteropodids was gathered in a primary tropical rain forest area in southern Negros Island, Philippines. Seeds and marked remains of food plants were collected: (1) in 1 m × 1 m seed traps laid out at 3-m intervals along four orthogonal transects around selected fruiting figs, and (2) randomly from the forest floor within a 100 m × 100 m area surrounding these trees. Identity of consumers was determined directly through visual observation and from netting around sampling trees and/or indirectly through analysis of palatal imprints on ejecta. Food habits were recorded for nine species of fruit bats: *Acerodon jubatus*, *Cynopterus brachyotis*, *Haplonycteris fischeri*, *Harpyionycteris whiteheadi*, *Nyctimene rabori*, *Ptenochirus jagorii*, *Pteropus hypomelanus*, *P. pumilus* and *P. vampyrus*. Figs (*F. Moraceae*) were found to be a major part of the diet of these bats in the area: at least 11 out of 30 *Ficus* species identified from the area were being eaten in varying amounts. Other components of the diet included fruits of 11 other plant species belonging to seven families. There was some evidence of consumption of leaves and moss. In general, data suggest differential choice of fruit along lines of fruit colour (i.e., bright versus dull-coloured fruits), on the basis of available crop density and on plant height. No size relationships between bats and the fruits consumed were evident.

Analysis of seed shadow patterns strongly indicates that feeding patterns differ between large-sized bat species (> 150 g body mass) and smaller species. Most splats and ejecta generated by large bats were concentrated beneath the crown of the source tree, indicating consumption of fruits on the tree itself. In contrast, smaller bats used feeding roosts in the immediate vicinity of, but not in, a focal feeding tree. Mixed-species seed clumps were found beneath these feeding roosts. This difference in behavioural patterns of fruit consumption causes a more heterogeneous pattern of seed scattering than would be expected of a single-taxon (i.e. fruit bats as a whole).

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visitor coterie. The potential importance of these fruit bats as seed dispersers in forests is further supported by seed germination tests; gut-passed seeds of *Ficus chrysolepis* show higher percentages of germination than do seeds from fruits or ejecta.

Introduction

Current data on the feeding ecology of pteropodid bats in the Philippines consist almost entirely of enumeration of food resources in secondary growth areas and cultivated fields and orchards (Guerrero & Alcala 1973; Alcala 1976; Rabor 1977). Except for an assessment of the impact of bat foraging activities on orchards (Guerrero & Alcala 1973), documentation and analysis of patterns of fruit resource use in forest habitats are lacking.

Not surprisingly, virtually nothing is known of the relationships between these frugivores and the plant communities with which they interact; thus, their role in forest maintenance and regeneration in the Philippines is largely unknown. Recent studies in the Philippines, however, are beginning to demonstrate strong relationships between forest habitats and fruit bat diversity and abundance (Heaney, Heideman & Mudar 1981; Heaney, Heideman, Rickart, Utzurrum & Klompen 1989). Most striking is an emerging dichotomy between geographically widespread species that are highly abundant in disturbed and cultivated areas and the Philippine endemics that are largely restricted to forest habitats. Given this relationship, a better understanding and knowledge of food requirements and patterns of resource use in forest areas are of critical importance for at least two reasons. Firstly, shifts in patterns of resource (food and roost) availability may accompany the conversion of forest habitats to agricultural cultivation, and exploitative extraction of forest products could seriously reduce the ability of forest-dwelling species to sustain viable populations through time. Secondly, any decline in numbers and diversity in these bat populations and assemblages could potentially affect the distribution and reproductive biology of those plants that are primarily bat-dispersed or bat-pollinated.

This study documents fruit use by Philippine fruit bats in primary forest habitats. I identified plant species consumed, and examined parameters that characterize patterns of resource use among the species of fruit bats present. I also assessed the impact and potential consequences of fruit consumption on the dispersal of seeds by analysing seed shadow patterns and seed germination tests. Seed dispersal analysis was centred primarily on *Ficus* (fig) species. Although figs are not among the resources listed in published diets of Philippine fruit bats, initial surveys of the forest area studied indicated their importance in the animals' diet.

Data collection and analysis

The study was conducted in a 320-ha forest area surrounding Lake Balinsasayao (9° 21' N, 123° 10' E) in the southern tip of Negros Island, Philippines.

Vegetation was typically of a lowland forest type with some montane elements from the level of the lake (850 m) to about 1050 m in elevation. Forest canopy averaged 15 to 20 m in height, although emergents of up to 35 to 40 m were present. The dominant tree species were *Shorea polysperma* and *Syzigium nitidum* (Antone 1983). Small patches of cultivated clearings, typically planted with cash crops (such as *Seachium edule*) and abaca (*Musa textiles*), were present at the edges of, and within, the forest. Drought conditions encompassed the period of the study, with mean monthly rainfall estimated to be 180.1 mm (Heideman & Erickson 1987).

Intensive field data collection was conducted for six months from April to September 1983, with periodic visits made in the months before and after this period over a span of one year. Ten focal sampling trees of the genus *Ficus* were initially selected, primarily on the basis of fruiting condition, i.e. the trees were in early to mid-stages of fruiting, with no apparent evidence of fruit consumption. Fruit samples in various stages of development were obtained and evaluated for size, wet mass, hardness and colour. Herbarium samples of bat-consumed plants were collected and submitted to the Philippine National Museum of Natural History in Manila for identification. Fig identifications follow Corner (1965).

Four 1 m (wide) × 25 m (long) belt transects were established from the base of each sampling tree radiating outwards in four general directions (N, E, S, W). Plastic sheets (1 m × 1 m), or 'seed traps', were laid out at every third metre along the transect length beginning from the tree base. Seed samples were collected from traps daily from the onset to the end of feeding visits. 'Night samples' consisted of those collected prior to 0800, after sheets were cleaned at dusk of the previous day. 'Day samples' consisted of those that accumulated between 0800 and dusk. Samples included partially consumed fruits or non-seed fruit parts and 'seed aggregates', i.e. defecated or spat-out pellets containing one or more intact seeds. Bat faecal material is referred to hereafter as 'splats' (after Janzen 1978) and the masticated pellets as 'ejecta'. All samples were examined for seed content to determine plant source. Additional data on diet composition were recorded from analysis of faecal material from some captured bats. Night samples were quantified and categorized into size classes of large, medium or small, to indicate size class of bat consumer. These categories reflect discrete subsets of species whose palatal/dental characteristics (distance measurements and dental formula) are clustered within subsets but distinct between groups (Utzurrum 1984). These subsets included three large-sized species, three that were medium-sized and two that were small-sized (Table 1). One species was 'intermediate' between large and medium classes.

Consumer identity was determined directly through visual observations (especially for diurnal feeders) and indirectly through sporadic two- to three-hour netting (between 1900 and 2200) around sampling trees and the analysis of dental and/or palatal imprints on ejecta and fruit parts. Information on

Table 1. Species checklist of pteropodid fruit bats by size categories^a

Species	Average forearm length (mm)	Body mass mass (g)	Size category ^b
<i>Acerodon jubatus</i> ^c	200	1000+	Large
<i>Pteropus hypomelanus</i>	138	450	Large
<i>Pteropus vampyrus</i>	190	1000	Large
<i>Pteropus pumilus</i> ^c	110	180	Intermediate
<i>Harpyionycteris whiteheadi</i> ^c	84	100	Medium
<i>Nyctimene rabori</i> ^c	75	60	Medium
<i>Ptenochirus jagorii</i> ^c	81	80	Medium
<i>Cynopterus brachyotis</i>	63	35	Small
<i>Haplonycteris fischeri</i> ^c	47	20	Small

^a Excluding 3 principally pollen- and nectar-feeding species: *Eonycteris robusta*^c, *E. spelaea*, *Macroglossus minimus*, and the typically non-forest species, *Rousettus amplexicaudatus*.

^b See text (p. 65) for explanation.

^c Species endemic to the Philippines.

consumers compared across a range of fruit types and characteristics was used to model patterns of fruit choice among the various bat species.

Three descriptive parameters are presented herein to characterize seed dispersal activities of the fruit bats: (1) the density-distance function (i.e. seed density index versus distance from tree source) of the seed shadows around three of the 10 sampling trees; (2) species composition of samples in seed traps; and (3) seed viability based on germination tests. The seed density index is derived from log-transformed counts of seed aggregates. Seed aggregate counts per square metre were first adjusted to correct for proportional oversampling closer to the tree base, as the proportion of area sampled to total area decreases with distance from tree base as a function of circular area. Thus, counts at each trap were multiplied by a factor, X , where $X = [1 \text{ m}^2 (\pi r_i^2 - A_p) / (\pi r_b^2 - A_t)]$, and where r_b = radius from base of tree to the first square, r_i = radius from base of tree to square to be adjusted, A_t = area of tree base, and A_p = area of sphere from midpoint of tree base to radius preceding square to be adjusted. All adjusted density counts were then log-transformed, $\log_{10} (\text{count} + 1)$, because of high variance in counts at each transect (Sokal & Rohlf 1981). Only seeds of the focal sampling tree are included in the seed shadow curves. 'Foreign seed aggregates', i.e. those belonging to plant species other than the species being sampled, are noted separately.

Seed germination tests were done on *F. chrysoplepis* following procedures described in Utzurrum (1984) and Utzurrum & Heideman (1991). The trials included 20 replicates of fruit seeds and 16 replicates each of splat and ejecta seeds. Each replicate contained 30 seeds. Mean germination percentages of these three seed types are compared by means of the Kruskal-Wallis test (Sokal & Rohlf 1981).

Results

Fruit consumption patterns

A total of 22 species of food plants were identified from fruit remains, splats and ejecta. These included 11 species of *Ficus* (F. Moraceae; Table 2) and 11 other species belonging to seven plant families (Table 3). These plants ranged from trees to shrubs and included understory vines (*Piper* spp.) and lianas (*Freycinetia* spp.). Of these 22 fruit resources, 54.5% bore green-coloured fruits, 22.7% had orange to bright red fruits, 18.2% were coloured deep red to dark purple (near black) and the remaining 4.5% (or 1) dull yellow-brown (Tables 2 and 3). Not all bats ate all these resources, but broad overlaps in diets were evident. Figs were found to be the major component of the bats' diets, especially of *A. jubatus*, *C. brachyotis*, *H. fischeri*, *N. rabori* and *P. jagorii*. Fruiting figs were abundant throughout the study period, and consumption of syconia did not vary quantitatively between months when no other resource of similar abundance was available (April to June) and months when fruits of *Syzygium* and *A. simplicifolia* were abundant (July to September). Fig consumption by frugivorous bats has been documented mainly in the Neotropics (Vásquez-Yanes, Orozco, François & Trejo 1975; Fleming, Heithaus & Sawyer 1977; Bonaccorso 1979; Janzen 1979; Morrison 1980; August 1981) and in some parts of the Old World tropics (Marshall 1983, 1985). For Philippine pteropodids these are the first documentations of the species consumed and the species of the consumer.

The 10 fig trees selected for intensive sampling were: *F. chrysoplepis* ($n=4$), *F. crassiramea* ($n=2$), *F. pubinervis* ($n=2$), *F. sumatrana* ($n=1$), and *F. cf. variegata* var. *sycomoroides* ($n=1$). Two of the trees aborted their crops prior to frugivore visits, including one of the *F. chrysoplepis* and one *F. crassiramea*. No evidence of bat visits was ever recorded for *F. sumatrana*. Very few, and only large-sized, seed aggregates of *F. crassiramea* were collected despite a qualitatively large crop, although moderate to heavy consumption of this fig by large bats has previously been noted (P.D. Heideman pers. comm.). Syconia of both *F. crassiramea* and *F. sumatrana* were coloured bright red, were relatively mushy upon ripening and had thin fruit walls (flesh). The other three species studied underwent heavy frugivore visits. Syconia of these species remained green upon ripening and retained a relatively firm consistency upon softening. Two species of fruit doves (*Phapitreron amethystina* and *P. leucotis*) and a hornbill (*Penelopides panini*) were recorded feeding on *F. crassiramea* on two occasions; day samples indicated the occurrence of other avian feeding visits. Flowerpeckers (*Dicaeum* spp.) and *P. amethystina* were seen feeding on *F. sumatrana* syconia. In all recorded instances of avian feeding, consumption took place directly on the tree. Visits lasted no more than 15 min. A group of four macaques (an adult pair and two juveniles) visited one of the fruiting

Table 2. Checklist of bat food resources in the Family Moraceae

Species	Syconium colour (basic)	Size index (L x W) (cm ²)	Tree height category	Crop abundance	Consumer size category ^a
<i>Ficus benjamina</i>	Red to purple	0.5	Canopy	High	Large
<i>F. crassiramea</i>	Bright red	3.8	Canopy	High	Large
<i>F. obscura</i>	Red to purple	0.4	Canopy	Moderate	Large
<i>F. recurva</i>	Red	0.3	Canopy	Moderate	Large
<i>F. aurantiacea</i>					
var. <i>parvifolia</i>	Yellow-brown	63.0	Canopy to emergent	Low	Medium, small
<i>F. chrysoplepis</i>	Green	8.1	Subcanopy/canopy	Moderate to high	Large to small
<i>F. congesta</i>	Pale green	4.4	Understorey	Low to moderate	Medium, small
<i>F. nota</i>	Green	1.7	Understorey	Low to moderate	Medium, small
<i>F. pubinervis</i>	Green	3.2	Canopy/emergent	High	Large to small
<i>F. septica</i>	Green	4.8	Understorey	Low to moderate	Medium, small
<i>F. cf. variegata</i>	Green	4.0	Subcanopy/canopy	High	Large to small
var. <i>sycomoroides</i>					

^aSee text (p. 65) for explanation of size categories.**Table 3.** Checklist of bat food resources: non-fig

Species	Fruit colour (basic)	Size index (L x W) (cm ²)	Tree height category	Crop abundance	Consumer size category ^a
Euphorbiaceae:					
<i>Aparosa simplicifolia</i>	Green	1.8	Understorey	Moderate to high	Medium, small
Melastomaceae:					
<i>Melastoma</i> sp.	Deep purple	1.0	Shrub	Low to moderate	Medium, small
Musaceae:					
<i>Musa</i> sp. (wild)	Green	36.0	Understorey	Low	Medium, small
Myrtaceae:					
<i>Syzgium</i> sp.	Pale green	3.2	Canopy	High	Large to small
Palmae:					
Species 1	Deep purple	1.2	Understorey	Low to moderate	Medium, small
Species 2	Orange to red	10.8	Understorey/subcanopy	Low to moderate	Intermediate, medium
Pandanaceae:					
<i>Freycinetia</i> sp.1	Reddish orange	72.0	Subcanopy/canopy	Low	Intermediate, medium
<i>Freycinetia</i> sp.2	Red	9.0	Understorey/subcanopy	Low	Medium
Piperaceae:					
Species 1	Yellow green	1.6	Understorey	Low	Small
Species 2 and 3	Green	1.5	Understorey	Low	Medium, small

^aSee text (p. 65) for explanation of size categories.

F. chrysolepis for two successive days when syconia were still very immature, i.e. seeds were very poorly developed. Figs were picked at random and all were discarded unconsumed. These two visits lasted 30 and 40 min each. An estimated 15% reduction in crop size per visit was associated with these two bouts.

Seed dispersal patterns

Density-distance curves for four transects of two *Ficus* species were chosen from among seven trees monitored to illustrate the heterogeneous nature of the shadows and the factors that may have influenced these variations (Fig. 1). The west transect of *F. pubinervis* shows a pattern of seed fall typical of seed shadows described by Fleming & Heithaus (1981): the majority of the seed aggregates fell in areas beneath the tree crown (Fig. 1a). Overall, beneath-crown seed density accounted for 75.9% of the total seed aggregates collected in all the four transects of this tree. The east transect of *F. chrysolepis* likewise showed heavy seed fall close to the tree base (Fig. 1b). In this case, however, the area of high seed density was extended over a wider area by the presence of a fruiting conspecific tree whose crown (indicated by dashed lines) abutted that of the sampled individual. The majority of seed aggregates in these two transects were accounted for by large bats, as shown by the partitioned curves (Fig. 1a, b). A G-test comparing the fall of large-sized seeds beneath the crown with that beyond the crown in seven of the *Ficus* trees studied showed significantly higher densities beneath the tree crowns (G test: $G_{\text{pooled}} = 61.29$, $P < 0.05$; Sokal & Rohlf 1981). These indicate that large bats primarily consume fruits on the source tree itself; the finding is in contrast to the generalization, based on Neotropical studies, that fruit bats are 'shuttling' foragers (Heithaus & Fleming 1978; Morrison 1978), a generalization likewise applied to Palaeotropical frugivorous species (Thomas, Cloutier, Provencher & Houle 1988). A second pattern is one in which the density remained relatively high or higher beyond the extent of the tree crown. In the north transect of *F. pubinervis*, this was primarily effected by small and medium-sized bats (Fig. 1c). The spikes in small and medium-sized seed aggregates beyond the tree crown indicate that smaller bats use temporary feeding roosts for processing fruits and thus exhibit a 'shuttling' feeding behaviour as opposed to the 'sit and feed' behaviour of large bats. Beyond-crown seed aggregates for seven trees of these two size classes were significantly more numerous than were those within the extent of the crowns (G test: $G_{\text{pooled}} = 217.06$, $P < 0.05$; Sokal & Rohlf 1981). Use of temporary night-feeding roosts has been documented for frugivorous species of phyllostomids (Heithaus, Fleming & Opler 1975; Bonaccorso 1979).

The south transect of *F. chrysolepis* followed a steep downhill slope of 30–40°. Seed aggregates falling in areas in the upper slopes closer to the

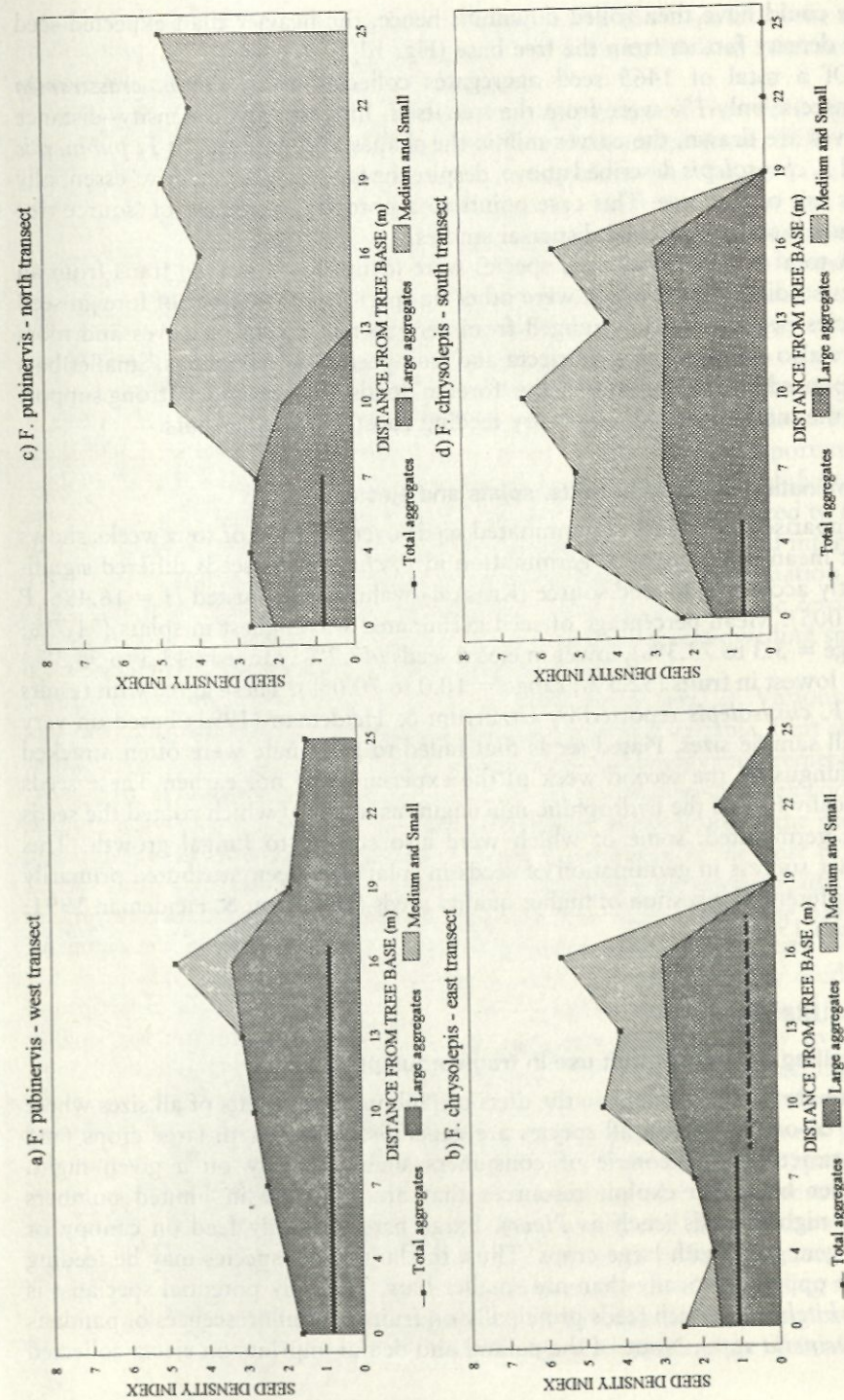


Fig. 1. Seed density-distance curves of four select transects of *Ficus chrysolepis* and *F. pubinervis*. (Solid lines indicate extent of tree crown along transect; dotted line represents crown of fruiting conspecific.)

tree could have then rolled downhill; hence, the heavier than expected seed fall density further from the tree base (Fig. 1d).

Of a total of 1465 seed aggregates collected from the *F. crassiramea* transects, only 1% were from the tree itself. Interestingly, if density-distance curves are drawn, the curves mimic the shapes and patterns of *F. pubinervis* and *F. chrysolepis* described above, despite the fact that the 'shadow' essentially was not of this tree. This case points to a potential weakness of 'source tree focused' analysis in seed dispersal studies.

A total of 13 foreign seed species were identified from seed traps from all trees studied, five of which were other fig species. The number of foreign seed species per tree shadow ranged from zero to ten. Ejecta of leaves and moss were also collected, as were ejecta and fruit peel of wild bananas. Smaller bats accounted for the majority of the 'foreign' loads. This provides strong support for the inferred use of temporary feeding roosts by smaller bats.

Germination of seeds in fruits, splats and ejecta

Comparison of counts of germinated seeds over a period of four weeks shows that mean percentages of germination in *F. chrysolepis* seeds differed significantly according to seed source (Kruskal-Wallis test: adjusted $H = 16.486$, $P < 0.005$). Mean percentage of seed germinated was highest in splats (71.7%; range = 3.3 to 73.3%), lower in ejecta seeds (47.7%; range = 13.3 to 93.3%) and lowest in fruits (32.5%; range = 10.0 to 70.0%). These agree with results for *F. chrysolepis* reported by Utzurrum & Heideman (1991) based on very small sample sizes. Plated seeds that failed to germinate were often attacked by fungus by the second week of the experiment, if not earlier. These seeds typically lacked the hydrophilic mucilaginous material which coated the seeds that germinated, some of which were also subject to fungal growth. This higher success in germination of seeds in splats has been attributed primarily to differential ingestion of higher quality seeds (Utzurrum & Heideman 1991; Janzen 1978).

Discussion

Modelling differential fruit use in frugivorous pteropodids

There are broad overlaps in the diets of Philippine fruit bats of all sizes where they co-occur. Almost all species are generalists. Trees with large crops tend to attract a wide coterie of consumers simultaneously on a given night. Smaller bats also exploit resources that are available in limited numbers on a nightly basis (such as *Piper*). Large bats primarily feed on canopy or emergent trees with large crops. Thus, the large-sized species may be feeding more opportunistically than are smaller bats. The only potential specialist is *H. whiteheadi*, which feeds principally on fruits and inflorescences of pandans (*Freycinetia* spp.). None of the palatal and dental imprints on ejecta collected

could be reliably traced to this species. Additionally, the majority of the seeds in faeces retrieved directly from captured individuals in this and other studies (P. Heideman, pers. comm.) are of pandan.

An examination of the basic characteristics of plants and their fruit against the range of bat consumers recorded to feed on these fruits reveals differential patterns of fruit choice among bats of various sizes (see Tables 2 and 3). Plant height and available crop density per tree are traits critical for large bats. Small to medium-sized bats, on the other hand, appear to discriminate primarily on the basis of fruit colour. Fruit size itself is not a consistent indicator of preference, contrary to the relationships between fruit size and bat size in the Neotropics (Heithaus, Fleming & Opler 1975). However, small, bright-coloured fruits are typically absent in the diets of bats less than 50 g in mass. Dull coloration is part of the suite of fruit traits forming the so-called chiropterochorous syndrome (van der Pijl 1957, 1982; Howe 1986). Analyses of the patterns of occurrence of this syndrome are important for understanding the evolutionary relationships between fruit bats and their food plants (Fleming 1979; Marshall 1983). Often overlooked is the need to focus on proximate factors underlying the relationship between preferred intakes of fruits and the possession of chiropterochorous traits. This examination is of equal relevance if we are to understand the importance of specific resources in the maintenance of fruit bat populations, especially forest-dwelling species that do not typically exploit cultivated orchard fruits.

Herein I present a qualitative model of food choice (Fig. 2). Various fruit traits associated with choice are expressed as a universal variable, fruit energy content. Predictions are based on the assumptions that energy requirements are a major factor influencing nightly foraging bouts and that feeding behaviour at fruit sources is indicative of the immediate energy expenditure of the species. Hence, for large bats, the principal energy expenditure is the cost of long flights to and among feeding areas or trees, since they are energetically more conservative at feeding trees (they eat at the tree itself). They are basically constrained by a need to maximize energy intake at each feeding tree or area and to acquire the proportionately greater total amount of energy needed to maintain a large body mass. They are predicted to feed on fruits of low to high energy content provided that the aggregate total of energy available per visit roughly equals or exceeds the cost of the visit to the feeding tree or area (Fig. 2). This requirement will be met by those plant species which provide moderate to large fruit crops per night, provided that such plants possess crowns directly accessible to approaches from open flight spaces (as in canopy and emergent trees). Medium to small-sized bats, however, with their characteristic use of temporary feeding roosts and shorter commuting distances (Heideman & Heaney 1989), are predicted to have higher energy expenditures associated with shuttling from fruit source tree to feeding roosts, even when such movements are combined with occasional commuting between local feeding areas. Thus, these smaller species are predicted to be flexible in

their choice along a wide range of crop density and other fruit traits, provided that energy intake per fruit will roughly equal or exceed the cost of shuttling between source and feeding roost (Fig. 2).

Additionally, I predict that the broad-scale dichotomy between bright-coloured figs and dull-coloured figs in the 'preference scale' of bats of all sizes in this study (with the latter apparently preferred over the former subset of available figs) will reflect qualitative and quantitative differences in the amounts of protein, fat and/or minerals present in these fruits. Fruit colour thus, coincidentally, indicates the underlying nutritional quality upon which choice is based and is not the basis of choice itself. Consumption of small fruits of low nightly availability is indicative of this sensitivity to the nutritional quality of fruits.

The types of comparative analyses needed to test these predictions relating energy and nutritional contents of food resources to fruit choice remain largely unexplored, especially in Palaeotropical frugivorous species of bats. Steller (1986) reported estimated daily energy and nitrogen requirements for *Pteropus poliocephalus*, but that estimation may not be truly reflective of diets in the wild. Although fruits rich in carbohydrates are quite common in the tropics, many are low in protein and nitrogen (Snow 1981; Fleming 1988), and available literature indicates that fruits typically consumed by bats are low in fat and protein content (e.g. Thomas 1982; Jordano 1983). I believe that this generalization requires re-examination, given that information on the nutritional quality is heavily biased by Neotropical data the majority of which are on bird diets. It remains to be seen whether the requirement for protein is in fact the factor that limits rates of consumption and, as a corollary, fruit choice, in pteropodid fruit bats, as proposed by Thomas (1984). No estimates

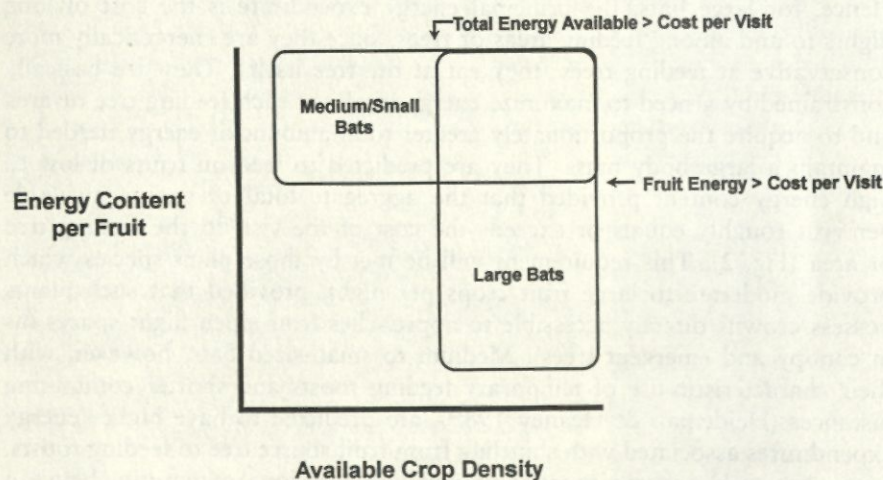


Fig. 2. Conceptual model of fruit choice in frugivorous pteropodids.

of energetic costs of foraging shuttles and commuting trips are available for pteropodids, although estimates for Neotropical species have been reported (e.g., Morrison 1978).

Seed dispersal and its implications for habitat maintenance and regeneration

The critical conclusion that may be inferred from the data on seed shadows and from the germination trials is that bats of different size categories contribute differentially to create a highly heterogeneous pattern of seed scattering. This heterogeneity is reflected in the form of mixed-species seed clumps within primary areas of seed fall from a feeding tree and in the variation in the shapes of seed-density curves. Seed shadows range from those characterized by high seed densities (principally single-peak shadows) beneath tree crowns (Fig. 1a, b), to shadows with extended tails of moderate seed density (Fig. 1c, d) and those with multiple local peaks (Fig. 1b, d). This heterogeneity is, perhaps, unique to the diversity of the bat dispersal coterie, with their attendant differences in feeding behaviour, and has been largely undocumented in Palaeotropical fruit bats prior to this study. Smaller bats, which are principally responsible for generating mixed-species seed plants, could strongly influence local patterns of seedling recruitment and regeneration. The importance of the tails of seed shadows for seedling recruitment and establishment have been discussed in recent literature (Coates-Estrada & Estrada 1988; Portnoy & Wilson 1993). If the observed numbers and types of non-bat tree visitors are indicative of the general disperser activity levels in this forest, especially for the subset of plant species studied, then bats could very well be the principal agent of seed dispersal in this and other sites. Although large bats deposit a majority of seeds in close proximity to source trees, they are probably important for successional patterns over a broader scale as they cover larger areas in their commuting to and from day roosts and between major feeding grounds (Rabor 1977; Heideman & Heaney 1989). The higher quality of seeds that are seen in splats reinforces the conclusion that large bats are important as agents of long-range dispersal, since the few seeds retained following feeding are those most likely to be taken over long distances.

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